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THE QUARTERLY REVIEW *of* BIOLOGY

THE PHYSIOGNOMY OF INSECTS

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Ante omnia scire convenit naturam corporis, quia alii graciles, alii obesi sunt; alii calidi, alii frigidiores; alii humidi, alii sicciores; alios adstricta, alios resoluta alvus exercet. Raro quisquam non aliquam partem corporis imbecillam habet.—*Celsus, Lib. I. Cap. III.*

AN ENTOMOLOGIST no less interested in his fellow men than in the insects may with increasing years of observation find increasing resemblance between the two—some insects seeming almost human and some humans behaving very much like insects. This may be due in part to the fact—if indeed it be a fact—that the entomologist may come to resemble the objects with which he is so constantly occupied. If we can trust the statements of some observers, he may even take on some of the physical peculiarities of the group in which he specializes. We have all known entomologists who looked like grasshoppers, cockroaches, bumble-bees or Histerid beetles. The confusion is increased by the fact—and this has not escaped the cartoonists—that there is a certain resemblance between the human and insect body, with its division into head, thorax, and abdomen. And although the insect body has too many appendages and certainly too many wings to suit any human being this side of Paradise, nevertheless the face, head, and eyes of some Orthoptera, Coleoptera, Hymenoptera, and Diptera are very suggestive of certain physiognomies which we daily encounter in the streets and trolley-cars of our great cities. In certain ancient entomological works, purporting to be of a serious character, for example in Jonston's *Theatrum universale omnium animalium* (1718), the heads of insects are often drawn with the obvious intention of accentuating their resemblance to human countenances.

HUMAN TYPES

Those who devote all their attention to our own highly polymorphic species, which Linnæus, I suspect, somewhat sarcastically called *Homo sapiens*, have repeatedly endeavored to group its various individuals in categories according to their temperaments and physical peculiarities. As a result, a number of human types have been distinguished and named

by a long series of investigators, most of whom agree that the pure types are best studied among the young adult males of the species. Two of the types, which have been recently called the "asthenic" and the "pycnic" by Kretschmer (1922), stand out conspicuously and will be recognized at once by the following diagnoses:

The asthenic is pale, scrawny, long-limbed, with narrow head and face ("hatchet-faced"), long, narrow, straight nose, small, often receding chin, narrow chest and abdomen, deficient development of fat and musculature, reduced pilosity on the body but often with abundant cranial thatch, abstemious, dyspeptic, with a tendency to tuberculosis, and when insane, schizophrenic, i.e., prone to fixed ideas, ideas of persecution, etc. This type is active, intense, intellectual, self-centered (introverted), often deficient in a sense of humor, fond of reforming, dogmatic or fanatical, and not infrequently detestable when claiming a too intimate knowledge of the Almighty's plans for making the world safe for democracy. The pycnic—so called, not because he likes picnics, though no other type is so fond of them—but from the Greek word πυκνός, meaning compact or thickset—is rubicund, rotund, large-bodied, short-limbed, broad through the chest, but broader through the abdomen, with round or pentagonal face, pug or thick nose, moderately pilose, fond of eating and drinking, eupeptic, with a tendency to apoplexy and arteriosclerosis; on the mental side cyclothymic, i.e., predisposed to the recurring, circular or manic-depressive forms of insanity, such as melancholia; extroverted, socially easy-going, tolerant in morals and religion and often very lovable because claiming no inside information in regard to the Almighty's designs.

These two types in their purity are sufficiently frequent among our American population. Kretschmer seems to have found the pycnics very common among the Swabians, who are generally characterized by the Germans as "gemütlich" or "gutmütig." The popular distrust of the asthenic and fondness for the pycnic is indicated by the fact that Satan, or Mephistopheles is usually represented as an asthenic while the favorite gods and saints of China and Japan are depicted as fat pycnics. When the belief in Satan was more vigorous than it is at present, he and his demons were often represented as belonging to the athletic type. [See the pictures from the twelfth to the sixteenth century and especially the frontispiece from Didron's *Christian Iconography* in Bonner (1913)]. Why the people should have chosen a symbol like Uncle Sam to represent the United States and one like John Bull to represent England was not altogether clear till the passage of the Volstead Act. Among historical figures the reader will recall Cassius (as depicted by Shakespeare), Dante, Savonarola, Torquemada and John Calvin as asthenics and Falstaff (as conceived by Shakespeare), Martin Luther and ex-President Taft as pycnics. In fiction Don Quixote and Sancho Panza are good examples of the two types. Bud Fisher's creation of Mutt and Jeff may also be cited in this connection.

The great mass of human individuals, however, may be regarded as blends or mosaics of the two types in varying proportions. Even during the lifetime of the same individual, the asthenic may predominate at one time, the pycnic at another. Often the young are asthenic and become pycnic with advancing years, and we have all seen examples of the reverse transformation of pycnic youngsters into asthenic oldsters. Undoubtedly the endocrine glands, and especially the thyroid, pituitary and interstitial glands,

are concerned in the production of both the extreme and the intermediate types.

Among the latter Kretschmer recognizes several categories. One of these is the "athletic," which I need not describe as the reader is familiar with its physical and mental peculiarities from the football and baseball field, the gymnasium, vaudeville stage and movies. Kretschmer further distinguishes "dysplastic" types, which show more or less pathological defect- or excess-development (hypoplastic or hyperplastic development) in certain characters, but I shall pass over these distinctions and for the sake of brevity and clearness call all the intermediates athletic.

The same or similar types have been recognized by other investigators and have been reviewed by Bauer (1924). The asthenic, athletic and pycnic types of Kretschmer evidently correspond to the phthisic, athletic and plethoric habitus of de Giovanni and to Beneke's microsomatic, microplastic, microskelic, longi-

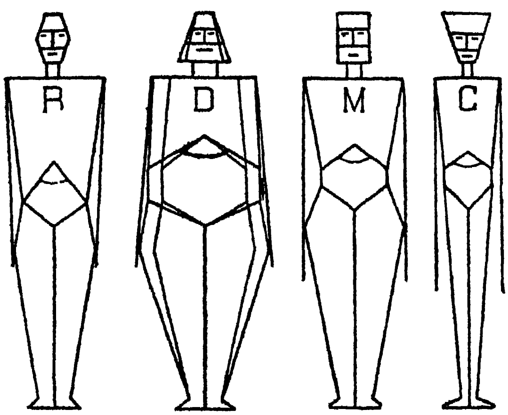

Fig. 1. The Four Human Types of Claude Sigaud, Schematized by Pierre Robin

lineus or longitypus and megalosomatic, euryplastic, brachyskelic, brevilineus or brachytypus, with the intermediate normosplanchnic, normosomatic, mesoplastic, normolineus, normotypus. The two extreme types correspond to Viola's microsplanchnic, or phthisic habitus and megalosplanchnic, or apoplectic habitus, to Bryant's carnivorous and vegetarian

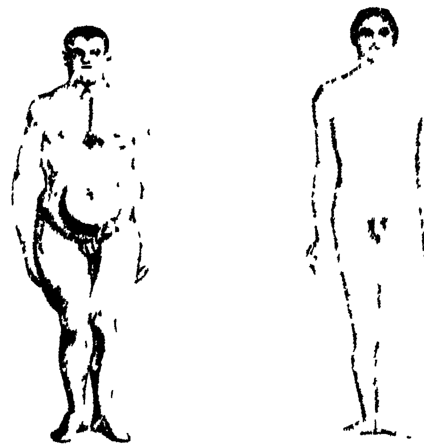

Fig. 2. Idealized "Round" and "Flat" Colloidal Human Types, According to MacAuliffe (Taken from A. Thooris: *La vie par le Stade*)

types, Bean's hypermorph and mesomorph types, Stockard's linear and lateral types, etc. Obviously the pycnic type is that of the human infant. According to Stockard (1923) "the linear type is the faster growing, high metabolizing, thin but not necessarily tall group, while the lateral type is slower in maturing and is stocky and rounder in form."

The French school, following Sigaud and including his pupils Chaillon, MacAuliffe and other contributors to the very interesting *Bulletin de la Société d'Etude des Formes Humaines*, recognize four human types, the respiratory, digestive, muscular and cerebral (fig. 1). The digestive corresponds to the pycnic, the cerebral to the asthenic, the muscular and respiratory to the athletic type of Kretschmer. In a recent paper MacAuliffe (1925) distinguishes a "round" and a "flat" type (fig. 2), which correspond to the pycnic and asthenic respectively, and refers their differences to differences in the col-

loidal state of their tissues, the former consisting of strongly, the latter of feebly hydrophilous gels. The cells of the bibulous pycnic have great osmotic powers, those of the asthenics a feeble surface tension. "The flat type functions more economically than the round. It is also probable that the electric polarization of the cellular surfaces is higher in this latter human category."

Bauer studied the distribution of Sigaud's four categories among 2000 male Viennese and found the following proportions of pure type: respiratory 18 per cent,

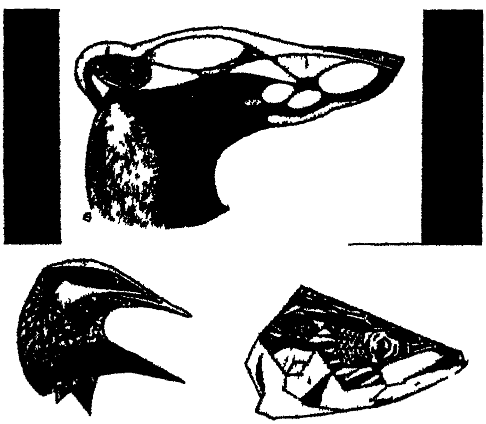

FIG. 3. HEADS OF GREY HOUND, BITTERN, AND PIKE TO ILLUSTRATE THE "FLAT" COLLOIDAL TYPE OF MACAULIFFE
(Taken from A. Thooris: *La vie par le Stade*)

muscular 9 per cent, cerebral 3.9 per cent, digestive 3.8 per cent. Taking the mixed forms in which one of the types predominates, he found: respiratory 43.1 per cent, muscular 23.8 per cent, cerebral 18 per cent, digestive 6.6 per cent. The remaining 8.5 per cent could not be included in any one of the categories. Zweig, one of Bauer's students, studying the same material disproved Sigaud's view that the types do not change with age, although it was clear that each is fixed in youth in its general characters. The digestive type increases with age. Sigaud's schema is not easily applicable to females. Bauer divides them according to the distribution of fat on their bodies into (1) "Reithosentypus" (with fat on hips); (2) fat on arms, breast and neck, but with thin legs; (3) fat on thighs and legs, but poorly developed on trunk; (4) fat on breasts and gluteal region (steatopygous type).

ANALOGUES OF HUMAN TYPES AMONG ANIMALS

Now it is interesting to note that all the main types exhibited by the single species *Homo sapiens* have their analogues in most groups of animals and even among the plants. As examples of the asthenics and pycnics I mention only the following: among our domestic animals the greyhound and King Charles spaniel (figs. 3 and 4) and among other mammals the giraffe and armadillo, among the birds the herons and finches (figs. 3 and 4), among reptiles the tree-snakes and box-tortoises, among the amphibians the coecilians and toads, among fishes the eels and box-fishes; among crustaceans such forms as *Caprella* and the crabs; among Echinoderms the brittle-stars and the sea-urchins; among myriopods *Geophilus* and *Glomeris* and among plants the vines and the melon-cacti. Between the extremes in each case we find the great majority of species, the athletes, which exhibit a more nearly average development of their organs.

Of course, the insects, which are represented on our planet by such a bewildering number and variety of highly specialized species, may be expected to show the asthenic and pycnic types in a very pronounced form. There are, in fact, in all the principal orders, whole genera or even families of the two types. For purposes of illustration I have brought together a series of these insect Mutts and Jeffs in the accompanying figures (figs. 5 and 6).

As the reader is familiar with them or with similar forms I shall not stop to designate the various tenuous walking-sticks, grasshoppers, ants, dragon-flies, crane-flies, mosquitoes, ant-lions, panorpids, etc., nor the many chunky bugs, beetles, moths, etc. The reader will notice that the latter insects, like some human pycnics, have large rotund bodies and rather short, slender legs, and will recall certain ently and often unsuccessfully wrestling with them, will certainly not object.

The general impression produced by the insect asthenics and pycnics is that of mutations which have somehow managed to survive among the great mass of athletic species, but it is doubtful whether they have arisen as such saltatory variations. The asthenics are more archaic or at least more frequent in ancient and

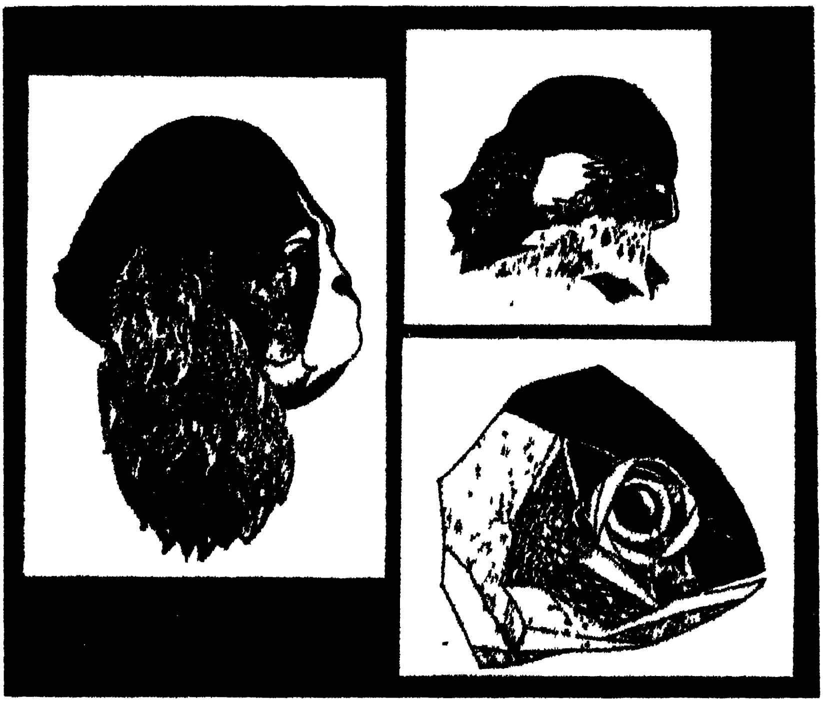

Fig. 4. Heads of King Charles Spaniel, Finch, and Bream, to Illustrate the "Round" Colloidal Type of MacAuliffe
(Taken from A. Thooris: *La vie par le Stade*)

cases of both types occurring in succession in the same species, as, e.g., in the ant-lion, which has a pycnic larva and an asthenic adult, and the flea which has an asthenic larva and a rather pycnic adult. Among the insects, too, the great majority of species are intermediate, and if I designate this group as "athletic" the economic entomologists, who spend their lives ard- primitive orders or suborders, and, with the exception of the mosquitoes and Chironomids, seem often to belong to rather rare, recessive or evanescent species. The differences between the two types cannot be due to the quality of the food, because there are predatory and phytophagous species in both groups. That they differ in metabolism is probable.

The pycnics, like their human analogues, are certainly great feeders compared with the asthenics—compare, e.g., the appetite of a dung-beetle with that of a walking-stick insect. And structurally there is a great difference in musculature, the muscles of the asthenics being long and slender while those of the pycnics are short and voluminous. This matter of the musculature in these and other insects—a matter as much neglected by recent insect morphologists as it was emphasized by those of former times—I should like to place in the center of the following discussion, because, as we shall see, it is the musculature that mainly determines the physiognomy of insects.

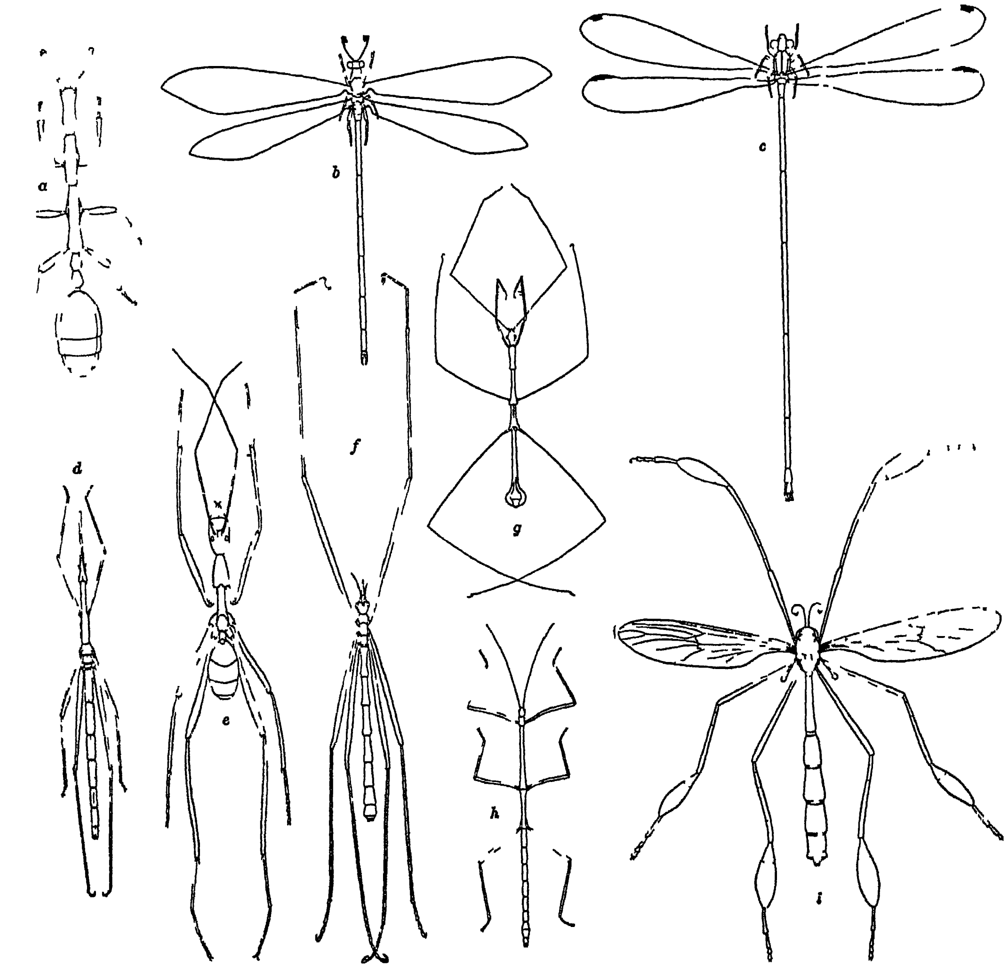

Fig. 5. Examples of Asthenic Insects Belonging to Various Orders

a, Staphylinid myrmecophile (Coleopteron); *b*, ant-lion (Neuropteron); *c*, dragon-fly (Odonate); *d*, grasshopper (Orthopteron), *e*, ant (Hymenopteron); *f*, Panorpid (Mecopteron), *g*, bug (Heteropteron), *h*, Phasmid (Orthopteron); *i*, crane-fly (Dipteron).

PRINCIPLES OF INSECT PHYSIOGNOMY

The reader is familiar with the fact that in insects, as in other arthropods, the musculature is inside the skeleton to

which it is attached and that the shape and size of the various elements of the skeleton depend on the volume and arrangement of the muscles. Here the skeleton and integument are one, whereas play of the musculature is visible from the outside, whereas in insects we are presented with a rigid envelope capable of movement only at well-defined, preformed articulations. Hence, also, the very lim-

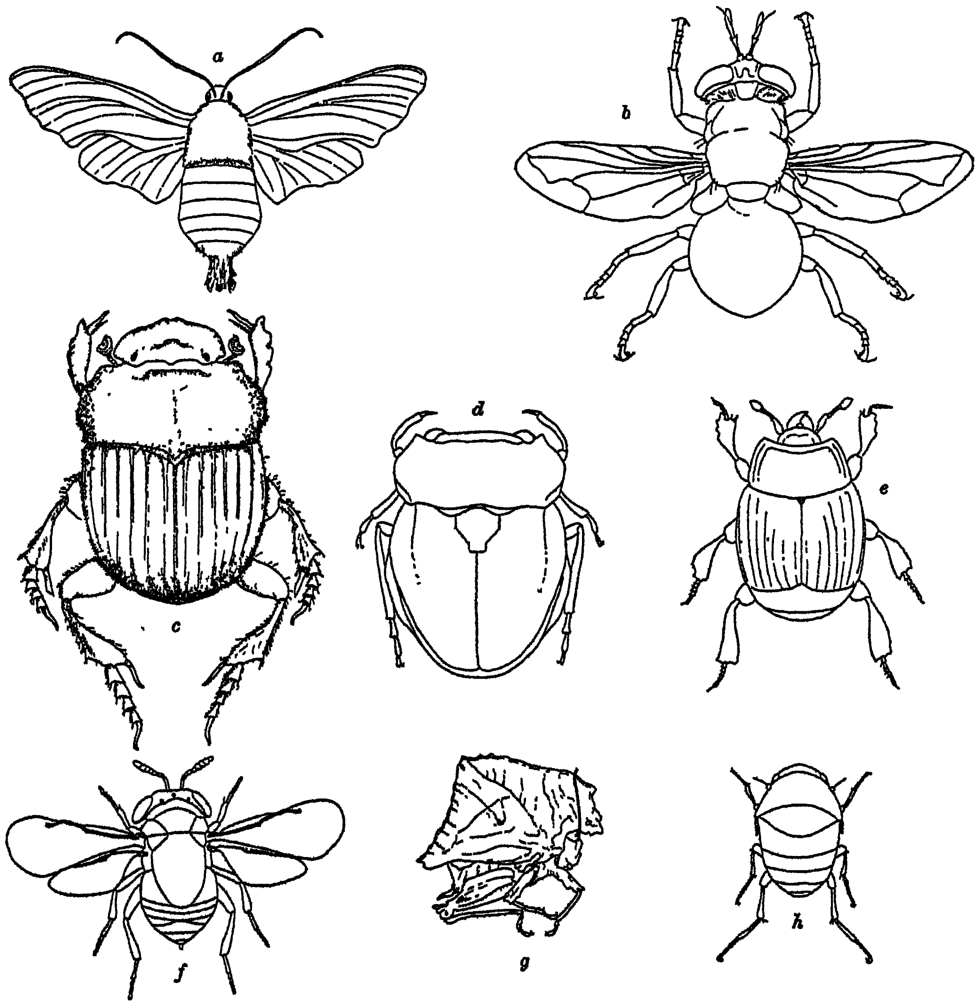

FIG. 6. EXAMPLES OF PYCNIC INSECTS BELONGING TO VARIOUS ORDERS

a, Sphingid moth (Lepidopteron); *b*, Syrphid fly (Dipteron); *c*, Lamellicorn beetle (Coleopteron); *d*, bug (Heteropteron); *e*, Histerid beetle (Coleopteron); *f*, Chalcidid fly (Hymenopteron); *g*, grasshopper (Orthopteron); *h*, Phorid fly (Dipteron).

in vertebrates the muscles which move the skeletal elements are external to them and immediately beneath the very flexible integument. Hence in vertebrates that are not too scaly, feathery or hairy the ited and mechanical expression of the emotions in insects as compared with the wonderful range and subtlety of expression in the human face and body, a range and subtlety so extraordinary that from

our earliest years it constitutes a means of intercommunication among us second only and very often superior to articulate speech. Moreover, although the powers of facial and bodily expression of the human infant are very limited compared with those of the adult, as we should see if we could follow the development of some great actor from his birth to his highest triumphs on the stage, the insect's expression throughout each of its instars is extremely uniform and circumscribed. Of course if we could look

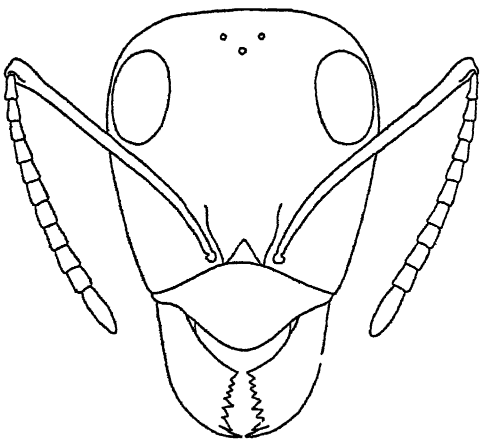

Fig. 7. Head of Worker of the Common Circumpolar *Formica fusca* L. from Above, Showing Eyes, Ocelli, Antennæ, Clypeus and Mandibles

beneath the rigid chitinous integument of such insect busybodies as ants, bees or solitary wasps we should probably witness an astonishing wealth of expression in the finer play of the smaller muscles, especially of those belonging to the viscera.

To trace the correlations between the development of the various muscles and that of the skeletal elements throughout the insect body would prove to be an undertaking as formidable as it would be wearisome. I shall therefore discuss at length only the most interesting region, the head, and confine myself still further very largely to a consideration of the ants. This will be best for two reasons: first, because I have been peering for nearly thirty years into the countenances of so many thousands of these insects that I have acquired some familiarity with their idiosyncracies, and second, because they are unusually favorable for physiognomic studies, owing to the extraordinary morphological and functional differences between the sexes and castes of the same species. The reader will have no difficulty in testing the general validity of my conclusions by extending them to the insects of other families with which he is acquainted.

The following are the main points which I should like to establish:

1. The form of the head and face is very largely determined by the size and shape of the flexor muscles of the mandibles and in turn the functional or adaptive peculiarities of these organs are closely correlated with the character of their flexor muscles.

2. In certain species, at least, the development of the antennal muscles seems to be correlated with the convexity of the front, or forehead.

3. The antennæ are also responsible for the development of certain adaptive structures in the configuration of the head, such as the scrobes.

4. The eyes are of little importance in determining the shape of the head in the workers and females of most ants, but these organs, when large, as in male ants and especially in certain other insects with haustellate mouthparts (Diptera, Lepidoptera, Mecoptera, Heteroptera, etc.) have considerable physiognomic value.

5. Certain head-forms are very largely determined by direct adaptation to the cylindrical cavities in the hard plant tissues or soil inhabited by the insects.

Let us begin with the head of our common *Formica fusca*, an ant of the true Nordic type, the *beau ideal* of the family, with chaste, well-balanced features and beautifully rounded forehead (fig. 7). To a slightly stretched imagination this head will not appear so very inhuman, especially if we let the clypeus represent the nose. The mouth is rather large, to be sure, and its upper lip is hidden away under the clypeus. The antennæ and mandibles, however, are decidedly inhuman. But if we imagine our hands and arms split into two pairs of appendages, and one pair thin, mobile, covered with exquisite, intermingled tactile and olfactory organs and inserted just above the base of our nose, and the other, shortened till only the rigid hands remain and inserted in the corners of our mouth, we should be equipped very much like an ant. And, no doubt, we should find the whole arrangement delightfully convenient. We could do very rough work with our inferior, or oral pair of hands without in the least impairing our sense of touch in the superior, or nasal pair, and the intimate combination of touch and smell in this pair would enable us to gain a very satisfactory knowledge of our immediate environment. We should move through the world like ants, continually topochemorecepting the various objects in our path, and we should probably speak of strawberries as soft, rounded-conical odors, of cigarettes as harder, cylindrical odors, table-tops as very hard, smooth, oblong odors of a certain quality, etc.

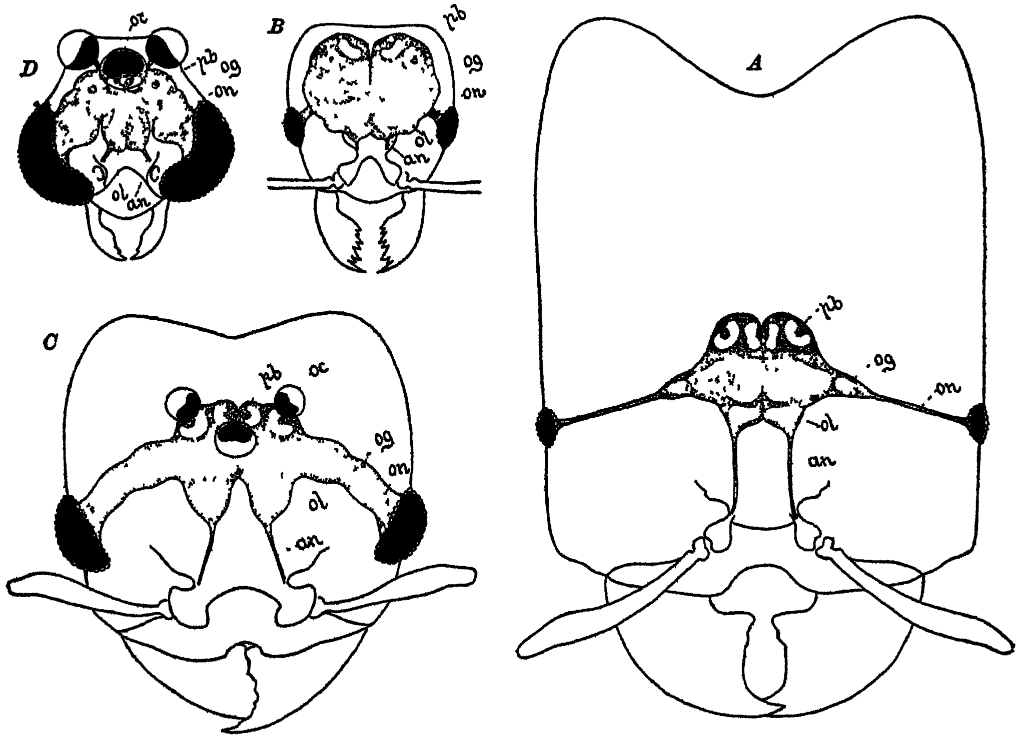

FIG. 8. HEADS AND BRAINS OF THE FOUR CASTES OF *Pheidole instabilis* EMERY FROM TEXAS, DRAWN TO THE SAME SCALE

A, soldier; *B*, worker; *C*, female; *D*, male

Judging by superficial appearances we might be tempted to extend the old phrenology of Gall and Spurzheim to the ant and regard the size and shape of its hard cranium as indications of the size and shape of its brain, but when we open its head we see at once that the brain is separated by a considerable space from the cranial wall and that the greater part of the cranial cavity is filled with muscular tissue. The brain varies greatly

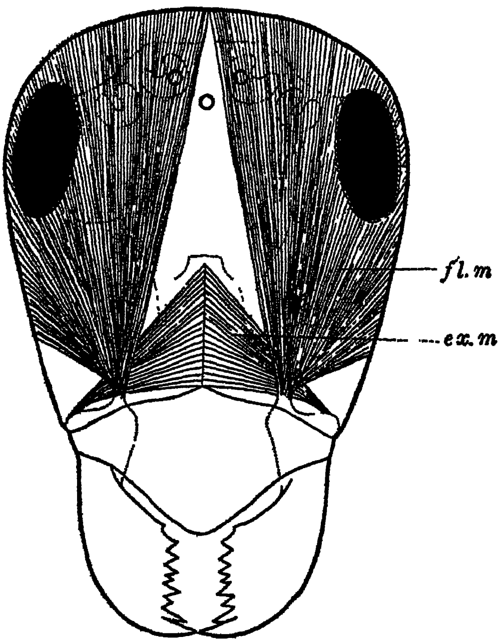

FIG. 9. HEAD OF WORKER *Formica fusca* L.
fl. m., flexor muscle of mandible; *ex. m.*, extensor muscle of same.

in different species and even in the different castes of the same species. Roughly speaking, the brain seems to vary inversely as the size of the individual ant. This is clearly seen in the heads of the four castes of a common Texan *Pheidole* (*Ph. instabilis*) (fig. 8). When the eyes are small or of moderate size, therefore, the head is an index to the muscular powers and not to the intelligence or sensory development of the insect.

CORRELATION OF HEAD SHAPE AND MUSCULATURE OF MANDIBLES

Returning to the head of *Formica fusca* (fig. 9) which has an unusually large brain, and removing the dorsal wall, we observe that on each side of the median line its contents consist very largely of a huge pyramidal muscle, which is attached proximally by a short, stout tendon to the inner corner of the base of mandible, while the gradually expanding fibres are attached distally to a very large area comprising much more than the posterior half of the cranial wall. In some ants this muscle, the contraction of which closes the mandible, really consists of two muscles, but as both have the same mandibular tendon and the same function, I shall treat them as a unit. It has been called the adductor, or flexor mandibulæ. The muscle which opens the mandible, the abductor, or extensor, is very much smaller. It is flattened and fan-shaped, inserted by a short, stout tendon on the outer corner of the extreme base of the mandible and runs ventrally under the tendon of the flexor to spread out and become attached to a thin, chitinous plate, or apodeme, which rises in the middle line from the floor or ventral wall of the cranium, the gula.

The great differences in the volume of the mandibular flexors and extensors is, of course, correlated with differences in their functions. The extensors have merely to open the mandibles, but the flexors have to perform the much more arduous task of seizing, holding, biting, gnawing or crushing the prey or the wood or soil in which the ants' nests are made. We may, therefore, concentrate our attention on this pair of more important muscles, whose development in the various species and castes intimately depends on the structure of the mandibles, and since the mandibles

differ greatly according to the habits of the ants it will be advisable to consider these appendages somewhat more closely. The typical mandible has a three-cornered blade, with a straight or more or less convex, entire outer border and two straight inner borders, one basal and toothless, the other apical and armed with teeth. A great many different types of mandibles may be recognized among the Formicidæ, but I will reduce them to nine: first, *biting* mandibles, of moderate size, very long, slender, with long apical border, armed with a few or numerous often unequal teeth (fig. 13–15); sixth, *clipping* mandibles, which are long, linear, straight or slightly curved, with a few sharp, abruptly incurved teeth at the apex, and the inner borders toothless, or finely serrate (figs. 16 and 17); seventh, *piercing* mandibles, which are slender, sickle-shaped and pointed, without teeth or with minute vestiges of them along the inner border (fig. 18*e–h*); eighth, *vestigial*

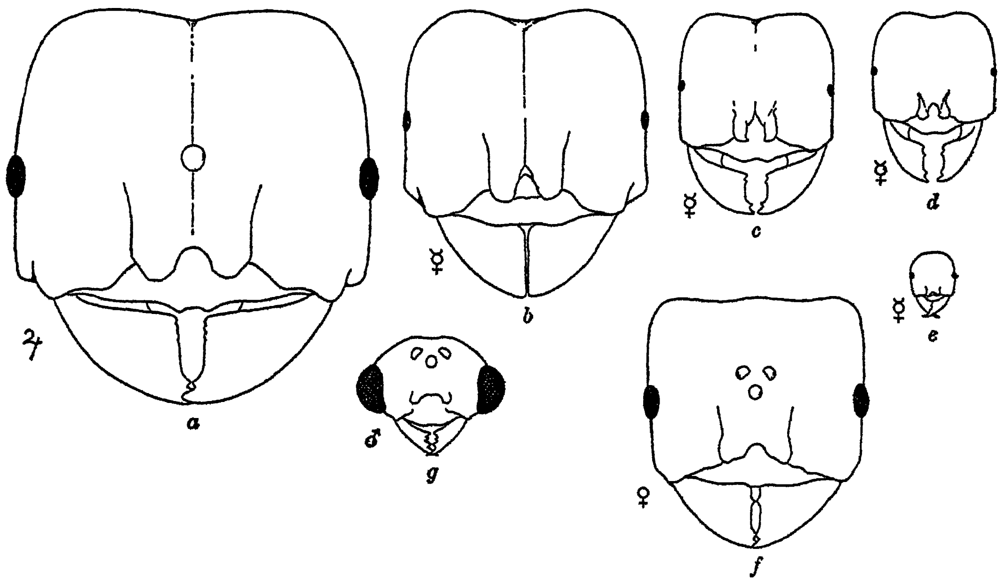

Fig. 10. Heads of Various Castes of an East Indian Harvesting Ant, *Pheidologeton diversus* Jerdon *a*, soldier; *b* to *d*, intermediate forms between the soldier and worker minima, *e*; *f*, female; *g*, male. Note rounding of occiput correlated with feeble mandibular development in the male and minima.

with subequal internal borders and a moderate number of sharp teeth on the apical border (figs. 7, 9, 12); second, *gnawing* mandibles, which are short and stout, with a few broad, strong teeth (fig. 12*a*); third, *crushing* mandibles, which are thick and stout, very convex externally, with few or no teeth (fig. 8a, 9a–d); fourth, *cutting* or scissor-like mandibles which are broad, flat and rather thin, with sharp, toothed apical border (fig. 11); fifth, *grappling* mandibles, which are mandibles which are reduced and apparently useless organs, occurring only in the male sex (figs. 10g and 17*b*); ninth, *aberrant* mandibles, including a number of singular forms of still unknown function (figs. 19 and 20). Of these various types, the biting, gnawing, crushing and cutting mandibles are large and powerful; the grappling, piercing, clipping, vestigial and aberrant though sometimes of large size are rather weak and therefore furnished with less powerful flexor muscles.

We may now examine several examples which show very clearly the correlation between the size and development of the mandibles, their flexor musculature and the shape of the head, a correlation so intimate that an expert mathematician might be able to express it in definite formulæ. In figure 21 I have represented the various castes of the harvester, *Pheidole instabilis*. The large individual and collects the seeds and stores them in the nest. The big-headed forms may be called the official nut-crackers of the colony because they crush the seeds with their mandibles. You will notice that the head decreases in size and length and in the convexity of its occipital lobes, as indicated by the gradual rounding of the posterior corners and decreasing concavity of the occipital border, till we reach the

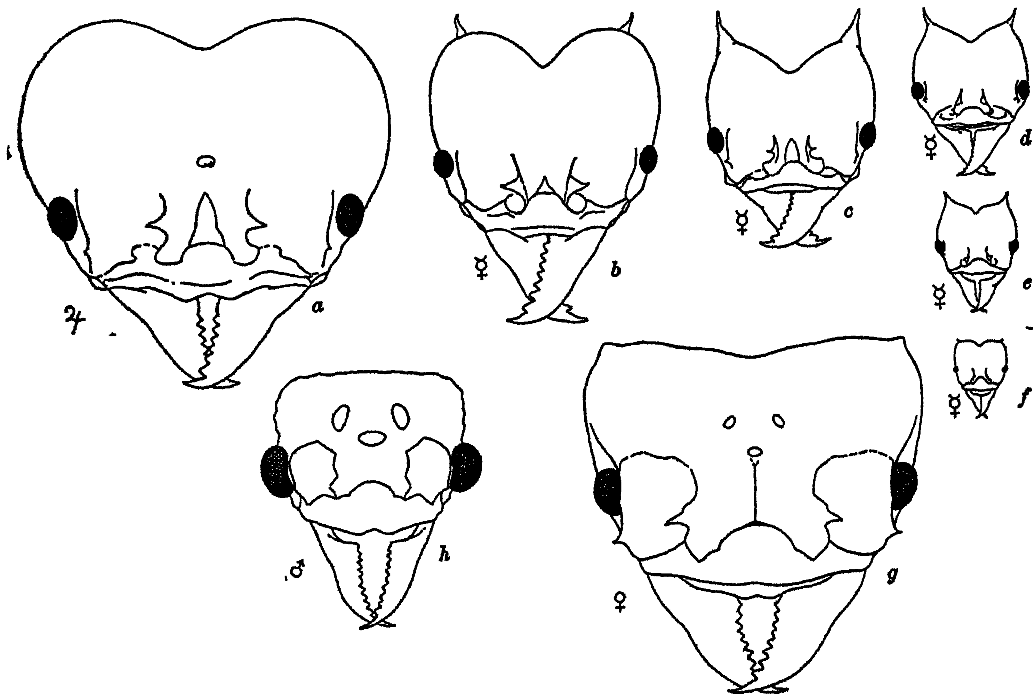

FIG. 11. HEADS OF THE VARIOUS CASTES OF A LARGE LEAF-CUTTING ANT, *Atta cephalotes* L. FROM THE NEOTROPICAL REGION

a, soldier; *b* to *f*, series of workers from the major to the minima; *g*, female; *h*, male. The strong mandibles in all the forms are correlated with prominent occipital lobes or angles.

below (*g*) is the deälated fertile female, or queen, the small winged individual (*h*) is the male; the very large-headed individual (*a*) is the largest type of worker, or soldier, the very small individual (*f*) the worker proper. Between these two extremes we find in any flourishing colony of the species, a complete graded series of intermediates, some of which (*b* to *e*) are represented. The worker (*f*) forages worker, which has a very small, rounded rectangular head, as broad as long. The crushing mandibles gradually become mandibles of the biting type as we pass from the soldier to the worker proper, and in my preparations the flexor muscles, which in all the forms fill out nearly the whole cranium, show a corresponding gradual decrease in volume.

The same phenomenon is exhibited in

the Indomalayan harvester, *Pheidologeton diversus* (fig. 10), but in an even more exaggerated form. In this figure only the outlines of the heads of a series of soldier and worker individuals and of the queen and male are represented. In the soldier provision is made for the huge flexor muscles by such a great increase in the width as well as in the length of the head, that the difference between the two extremes of the worker series becomes enormous. The queen's head (*f*) resembles that of the soldier (*a*) but you will notice that the male (*g*), which has small mandibles, has a small, broad head, with very short and rounded occipital region.

Another instructive example is furnished by the large leaf-cutting and fungus-growing ants of the neotropical genus *Atta* (fig. 11). Among these the head of the biggest workers, or soldiers (*a*) is not only greatly enlarged but its front and occipital lobes are extremely convex. The leaves are cut by the intermediate worker castes (*b* to *e*) with the scissor-like mandibles, whereas the smallest workers (*f*) never leave the nest but live among the delicate hyphæ of the fungus-gardens, weeding out deleterious spores and alien mycelia. This caste, which therefore works only on soft materials, has small, weak mandibles and the head is accordingly very much smaller, narrower and less convex. The queen (*g*), which has to dig her nest in the soil and defend her young brood, has a head much like that of the larger workers. The male (*h*), unlike most male ants, has well-developed mandibles and therefore exhibits a much greater development of the head behind the eyes.

The series of worker ants which I have used for illustration recalls the graded series of Harvard professors who have been classified by some of the students as high high-brows, high-brows, low high-brows, high low-brows, low-brows and low low-brows. Some authors regard the soldiers, the highest high-brows of our ant series, as monstrous, or pathological forms on account of the excessive development of their crania. Certain facts might seem to lend support to such an

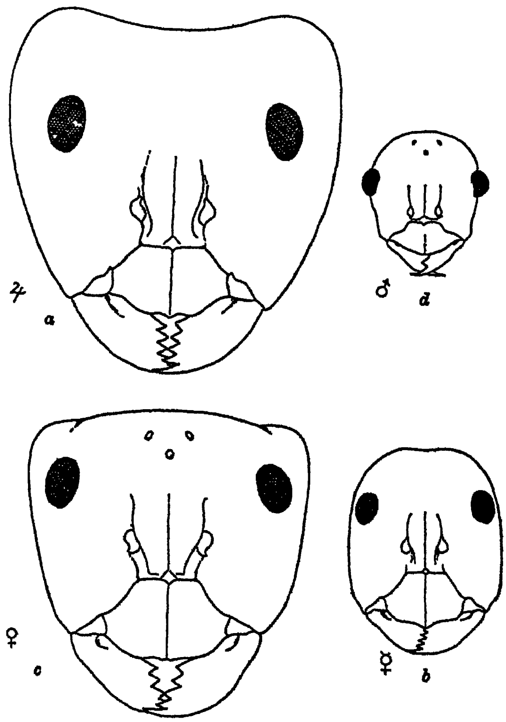

Fig. 12. Heads of Four Castes of an Australian Formicine Ant, *Camponotus* (*Myrmosaulus*) *bellicosus* Forel

a, worker maxima; *b*, worker minima; *c*, female; *d*, male. Note prominence of occipital corners in *a* and *c* with large mandibles and rounding of occiput in *b* and *d* with feeble mandibles.

opinion. If the soldier of *Ph. instabilis* be placed on its head on a perfectly smooth, hard, horizontal surface, the insect may be quite unable to right itself and may even die standing on its head. But this is a typical laboratory experiment. In its natural environment the soldier never encounters such surfaces. Closer study shows that all these sup-

posedly monstrous forms are really exquisitely specialized and adapted for the functions they have to perform in the life of their respective colonies. The soldiers of the harvesting *Pheidoles* and

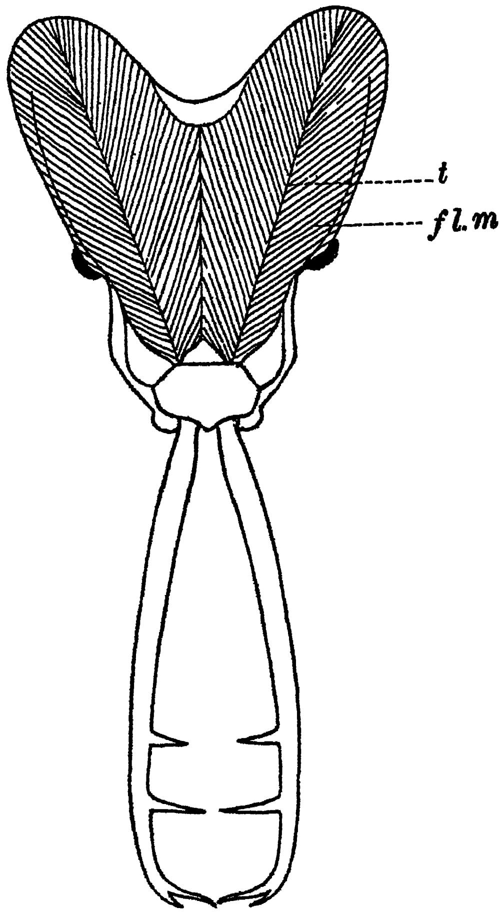

FIG. 13. HEAD OF *Strumigenys* SP., WORKER, SHOWING THE LONG GRAPPLING MANDIBLES, WITH THEIR FLEXOR MUSCLE FIBRES (*fl. m.*), AND THE PINNATE ATTACHMENT OF THE LATTER TO THE TENDONS (*t*.)

Pheidologetons are needed not only as seed-crushers, but those of the latter genus have another very different function. Several observers have seen groups of the minute *Pheidologeton* workers sitting quietly on the huge heads of the soldiers and riding to and from the nest. The soldiers of the insect-eating *Pheidoles* dismember the tough prey before or after

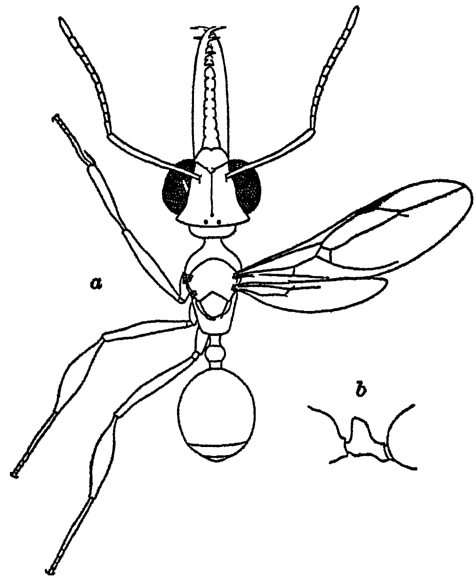

FIG. 14. *Myrmoteras donisthorpei* WHEELER, A FORMICINE ANT FROM BORNEO
a, female; *b*, petiole. Note the grappling mandibles and huge eyes

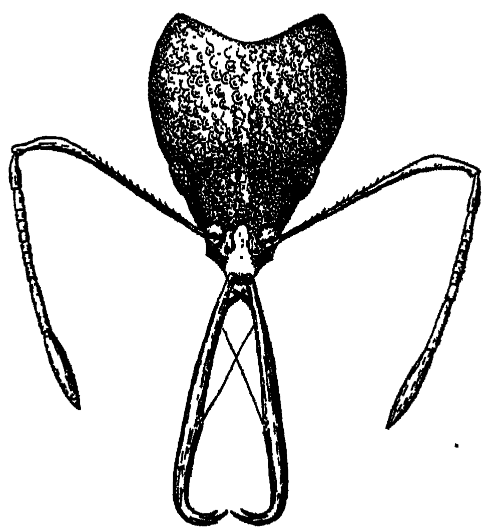

FIG. 15. HEAD OF *Acanthognathus lentus* MANN FROM CENTRAL AMERICA
(After Mann)

it has been carried into the nest. Hingston (1922, p. 61 et seq.) has recently

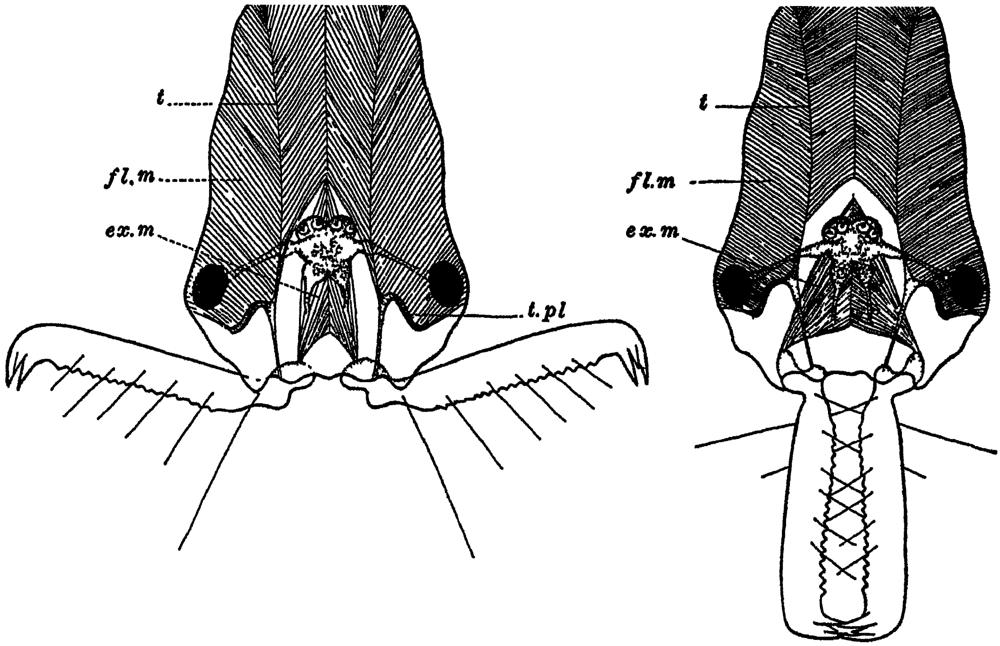

FIG. 16. HEAD OF *Odontomachus vastatus* F. WITH MANDIBLES OPEN AND CLOSED

ex. m., extensor muscles of mandibles; *fl. m.*, flexor muscles of latter; *t.*, tendon; *t. pl.*, plate of tendon

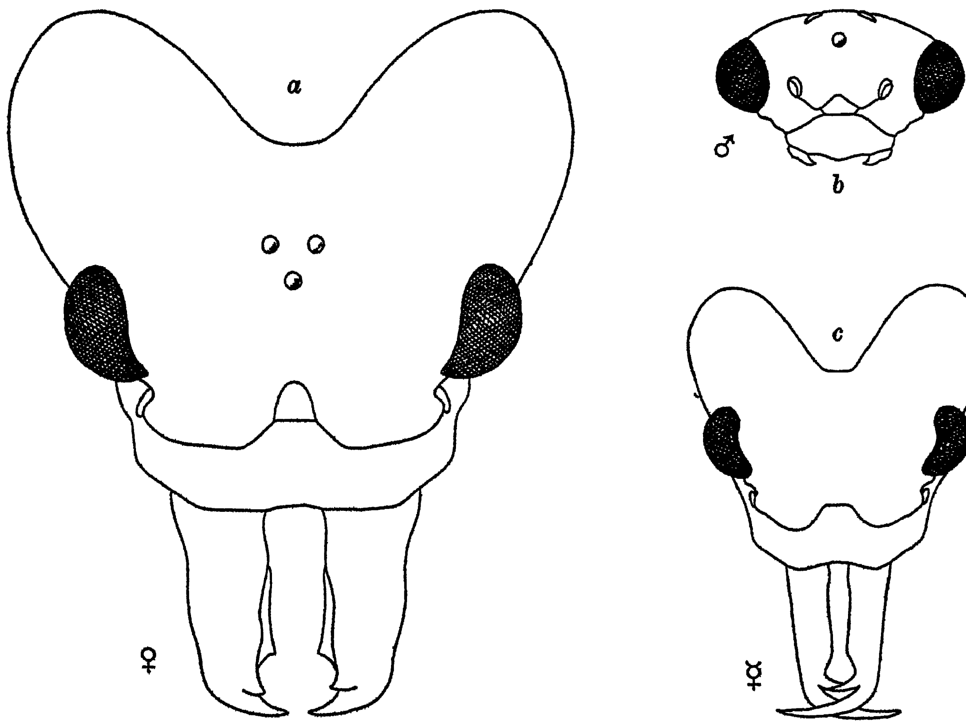

FIG. 17. HEADS OF SOUTH AMERICAN ANT, *Daceton armigerum* PERTY, WITH CLIPPING MANDIBLES

a, head of female; *b*, of male; *c*, of worker. Note the absence of occipital development correlated with vestigial mandibles in the male.

described in vivid language the extraordinary powers of communication exhibited by the diminutive *Pheidole indica* worker when notifying the soldiers to come out of the nest and oversee the transportation of the prey. As I have noticed a somewhat similar behavior in some of our American *Pheidoles* in the Southwestern States, I will quote part of his remarks:

As soon as a worker discovers a caterpillar or other suitable material for food, it proceeds to make a careful examination of its prey. It runs all over the caterpillar exploring it with its sensitive antennæ, shaking it with its jaws and attempting to drag it to the nest. The worker, satisfying itself that the discovery is suitable for storage and finding the removal of it beyond its own weak efforts, hastens off to the nest in great excitement and by the shortest route. It meets another worker on its path; their antennæ meet; the second worker is imbued with the enthusiasm of the first, has received information of the discovery and hastens off to the insect. A third, a fourth, and possibly more workers are similarly informed on the route and all hurry away to lend their assistance. But the excited discoverer hastens on to the nest. Now it has reached the entrance. It enters and is lost to view. In a few seconds a swarm of rushing, bustling and excited ants, come dashing headlong from the nest. From the way they are all lying in readiness just within the door and emerge at the same moment in one body as though they were awaiting a call for aid, I have no doubt but that these ants so divide their labor that certain workers are detailed for the duty of discovering food, and others, under the guidance of the soldiers, are under orders to remain in permanent readiness within the door of the nest to hurry out and render assistance when news arrives that a discovery has been made.

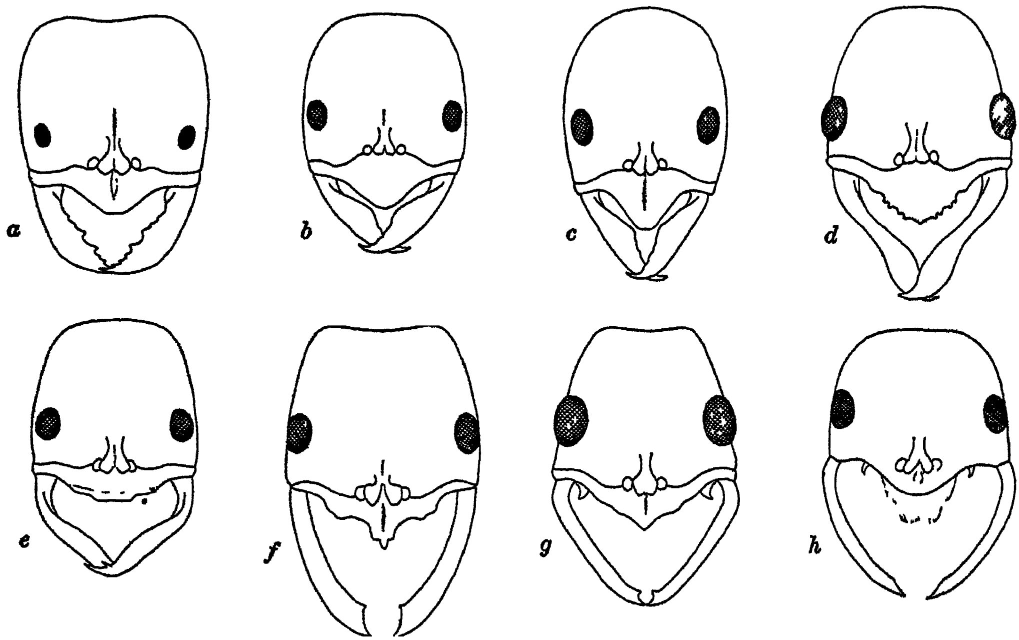

FIG. 18. HEADS OF EIGHT SPECIES OF *Leptogenys* (SUBGENERA *Leptogenys*, *Lobopelta*, *Odontoponera*, AND *Machaerogenys*), SHOWING CORRELATION OF FEEBLE MANDIBULAR DEVELOPMENT WITH NARROWING AND ROUNDING OF OCCIPITAL REGION OF HEAD

The news has come. Out they swarm in a dense throng preceded by the soldiers. Without the slightest hesitation they hurry over the ground, passing and repassing one another in their excited haste. . . . . On all sides they besiege the larva, which tries in vain by violent contractions to throw off its enemies. The battle grows hot and fierce. The caterpillar in its struggles now gains the mastery, but ants hurrying on in increasing numbers gradually overpower it. Workers, at intervals, retire from the battle and hasten back to the nest at the greatest speed to call out more reinforcements and hurl them into the

> fight. The caterpillar weakens; it cannot face these repeated additions to the strength of its foes. It is overwhelmed by the force of numbers, soon becomes exhausted, and then lies at the mercy of the ants which, clinging in a body round their powerless victim, drag it slowly to the nest.

Hingston also describes the peculiar behavior of the soldiers during migration to a new nest.

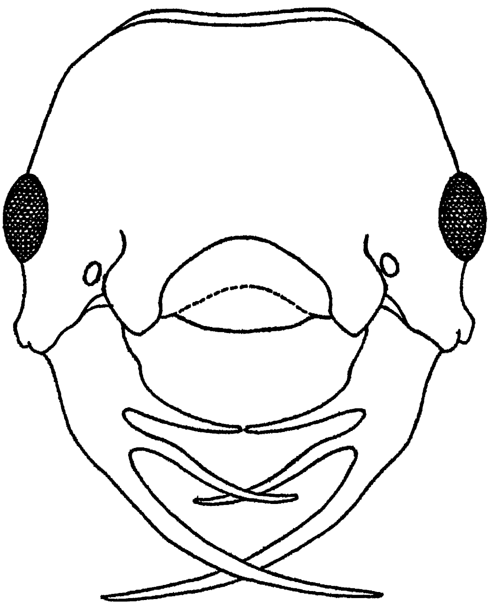

FIG. 19. HEAD OF WORKER OF THE NEOTROPICAL *Thaumatomyrmex ferox* MANN, WITH WEAK, ABERRANT, THREE-TOOTHED MANDIBLES AND UNDERDEVELOPED OCCIPITAL REGION

> The main burden of toil falls on the smaller workers. It is they alone that transport the larvæ, and they often carry their companions from nest to nest. The soldiers carry nothing. They are not humble toilers, but are the directors of the transport. They are the aristocracy of ant life. They hurry out of the nest singly and at intervals with a throng of laden ants following in their rear, and as each powerful soldier hastens along the migrating line it looks like an officer leading and directing his company of men. Nor do the soldiers return again to the old nest. The smaller workers, once they have deposited their larvæ in the new nest, hasten back for a fresh burden, but a returning soldier is never seen. It, no doubt, busies itself with important duties within the new nest, but takes no further part in the migrating line.

It may be readily shown that the conditions sketched for the cranial physiognomy of ants obtain also in other groups of insects, and especially among the Coleoptera. Two examples must suffice. Among many Lucanidæ, or stag-beetles (fig. 22) we find series of forms closely analogous to those of *Pheidole*, *Pheidologeton* and *Atta*, but in the beetles it is the males that are polymorphic. They

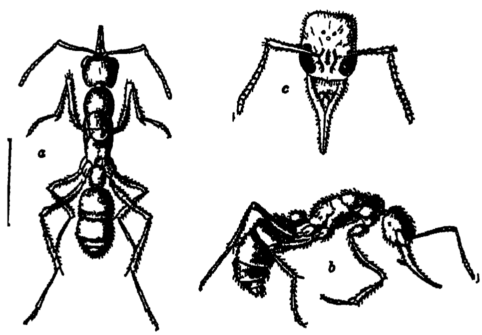

FIG. 20. A JUMPING PONERINE ANT, *Harpegnathos venator* VAR. *rugosus* WITH ABERRANT MANDIBLES, FROM HONGKONG

a, dealated female, dorsal view; *b*, same, lateral view; *c*, head, from above. (After G. May.)

have been arranged according to the development of the mandibles in series beginning with large macrodont forms, passing through amphiodont, eopriodont and priodont forms and ending with individuals with small mandibles like the female (Griffini, 1905, Champy, 1924). In such a series the head gradually decreases in width *pari passu* with a reduction in the size of the mandibles. There is also a corresponding reduction in the volume of the prothorax and fore legs. This occurs also in the ant series and might be expected, because the muscles that raise, lower and rotate the head are situated in the prothorax. In the highest highbrows among the Lucanids we even find the posterior corners of the head pro-

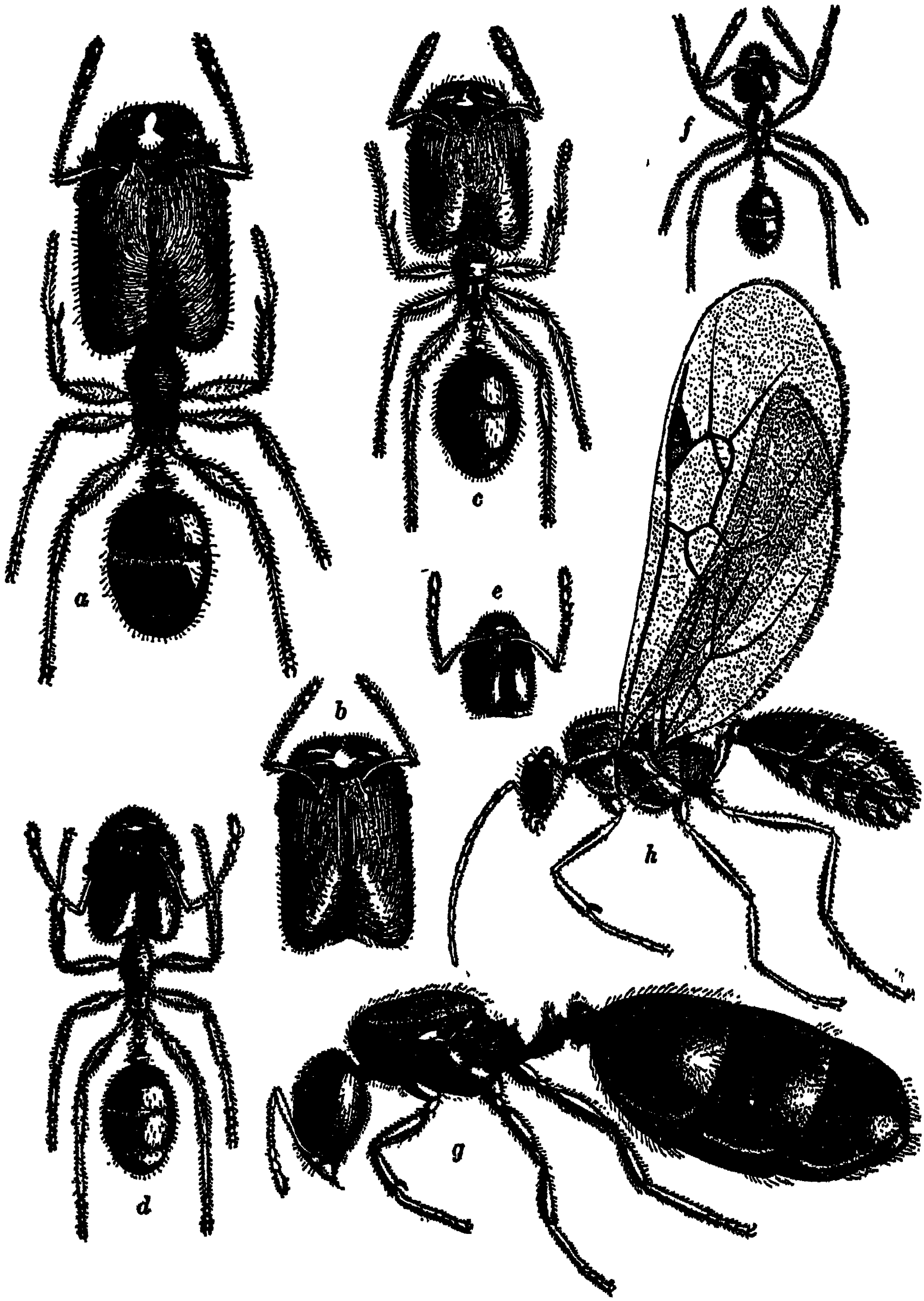

Fig. 21. Various Phases of a Small Harvesting Ant, *Pheidole instabilis*, from Texas

a, soldier; *f*, worker; *b–e*, forms intermediate between soldier and worker; *g*, female (deälated); *h*, male. All the figures are drawn to the same scale.

vided with crests or protuberances which increase the surface for the insertion of the enormous mandibular flexors and are therefore analogous to the bony crests on the skulls of many mammals that have powerful jaws and temporal muscles.

The correlation between the size and shape of the mandibles, head and pro-

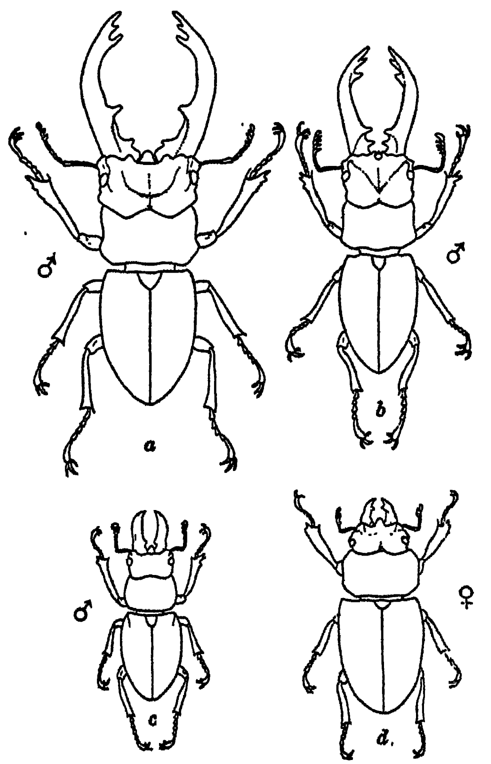

FIG. 22. FORMS OF A LUCANID BEETLE, *Metapodontus umhangi* FAIRM

a, heteromorphic male; *b*, intermediate male; *c*, homœomorphic male; *d*, female. (After Planet.)

thorax is also clearly shown by a comparison of the male and female *Eupsalis minuta* (fig. 23). In the specimens figured, whose bodies behind the prothorax happen to be of the same size, you will observe that the prothorax is shorter and anteriorly narrowed in the female in correlation with the much smaller head and mandibles. The slender prolongation of the head in this sex is specially adapted for oviposition. The huge mandibles are used by the male Lucanids in their fierce sexual contests, which have been witnessed by many observers. The males of Eupsalis also fight with their mandibles, though according to Leconte and Horn (1876) their combats are bloodless and "seem, so far as the records go, to be actuated rather by

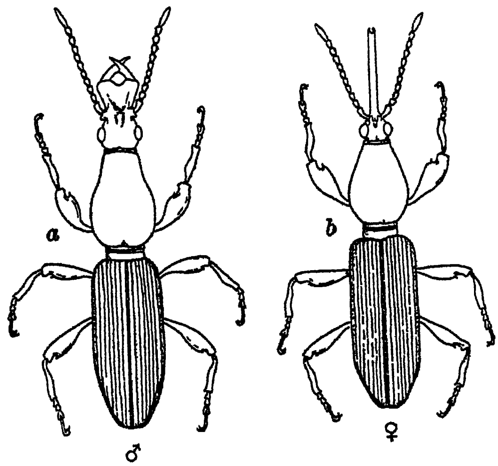

FIG. 23. A NORTH AMERICAN BRENTHID BEETLE, *Eupsalis minuta* DRURY

a, male; *b*, female

chivalric sentiment, than by animal passion." According to Blatchley and Long (1916, p. 21):

> Smith says that when the beaks of the females become wedged, as they sometimes do, the males use their forceps-like jaws to pull them out, but Riley states that the male helps in removing the beak by "stationing himself at a right angle with her body and pressing his heavy prosternum against the tip of her abdomen, her stout fore legs thus serving as a fulcrum and her long body as a lever."

After this digression I return to a consideration of some other types of heads and mandibles among the ants. Even in the smallest workers of the species hitherto described the mandibles are moderately strong and of the typical biting type, but in species that feed on

soft substances and excavate their nests in soft soil or very rotten wood or merely occupy cavities made by other insects, the mandibles may be weak and narrow and the head not only elongate and rounded behind but drawn out into a distinct neck. Among the best examples of this condition is *Apterostigma pilosum*. This ant, though related to *Atta*, does not nest in coarse ground and cut leaves but lives in cavities under bark or stones and makes its fungus gardens of insect excrement. Similar types of head (fig. 24*c*, *d*, *h*) occur in other asthenic species belonging to very different genera (*Aphaenogaster*, *Dolichoderus*, *Leptogenys*, *Leptomyrmex*) either as the only type among the workers or in the worker minima of species which have a large-headed soldier or worker maxima (*Dinomyrmex*, *Pheidole*, *Ischnomyrmex*).

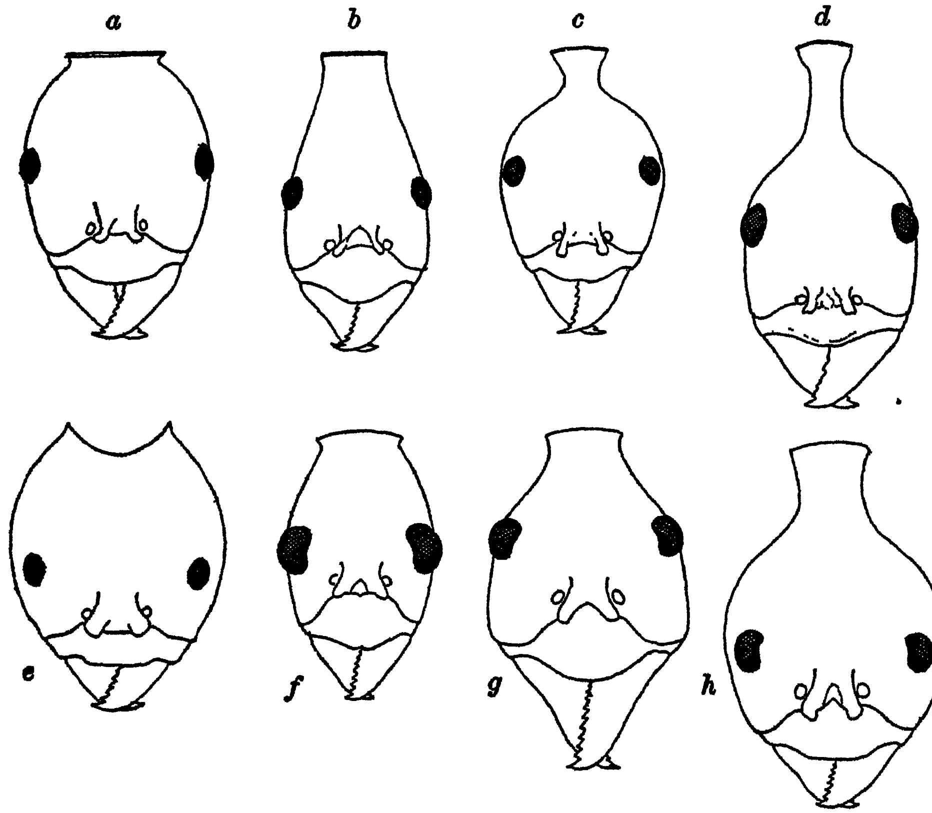

FIG. 24. PARALLEL DEVELOPMENT IN THE CONTRACTION OF THE OCCIPITAL REGION IN OLD WORLD SPECIES OF *Aphaenogaster* (*a–d*) AND NEOTROPICAL SPECIES OF *Dolichoderus* (*e–h*)

a, *Aphaenogaster* (*Nystalomyrma*) *longiceps* Sm. (Australia); *b*, *A.* (*Deromyrma*) *phillipsi* Wheeler and Mann (Palestine); *c*, *A.* (*Deromyrma*) *swammerdami* Forel (Madagascar); *d*, *A.* (*Planimyrma*) *loriai* Emery (New Guinea); *e*, *Dolichoderus decollatus* Sm.; *f*, *D. imitator* Emery; *g*, *D. rugosus* Sm.; *h*, *D. attelaboides* Fabr.

The grappling and piercing mandibles are also comparatively weak organs. The former, which are well-developed in certain Ponerinæ like the "bull-dog" ants of Australia and the species of the peculiar genus *Mystrium* are adapted for holding onto the prey while the abdomen is being bent around and the powerful sting inserted. Large hook-like mandibles

which seem to combine the functions of grappling and piercing organs are found in the soldiers of some of the army ants (*Eciton sens. str.*) (fig. 25*a*) although the next lower grade of worker (*b*) has curved, grappling mandibles and the smaller and far more abundant worker forms have cutting or biting mandibles (*c*, *d*). Both in our slave-making "amazons" of the genus *Polyergus* and in certain other genera (*Strongylognathus* and *Leptogenys*) the mandibles are of the true piercing type. The amazons use them for perforating the heads of their enemies and the species of *Leptogenys* (fig. 18*d–h*) evidently kill the soft-bodied termites, on which they prey, in the same manner. It will be noticed that the posterior portion of the head is distinctly narrowed and rounded in these various forms.

A highly specialized condition obtains in the clipping mandibles which show some extraordinary convergent developments in genera belonging to three different subfamilies of ants (the Odontomachii (fig. 16) among the Ponerinæ, the Dacetonini among the Myrmicinæ (fig. 17) and the Myrmoterini among the Formicinæ (fig. 14)). *Odontomachus* may be selected for more detailed description (fig. 16). The numerous species, known as clicking ants ("fourmis tic") in the tropics, have singular, elongate-subhexagonal heads, with the eyes placed far forward on lateral eminences while the mandibles are inserted close together at the anterior end of the head and consist of long, parallel-sided blades, with a few powerful, abruptly inflected terminal teeth and on their inner border a series of serrate denticles and long sense-hairs. The insect has a curious method of employing these organs. When it is excited they are widely opened as in the figure, and as soon as the long hairs, which act as triggers, touch an object, the blades are closed with lightning rapidity and an audible click. If during the closure their tips happen to strike against a hard body the insect is thrown off its feet and backward through the air to a distance of several inches. On opening an *Odontomachus* nest on a hot day one may hear a series of sharp clicks and find that the whole colony has suddenly evaporated into the surrounding vegetation. When the worker is hunting it cautiously approaches its insect prey with wide-open mandibles, suddenly darts forward, clips off an appendage and then retreats. It again advances and clips off another leg, antenna or wing and keeps repeating the performance till it has reduced its prey to a helpless, easily mastered torso. [For additional notes on the habits of Odontomachus see Wheeler (1900).]

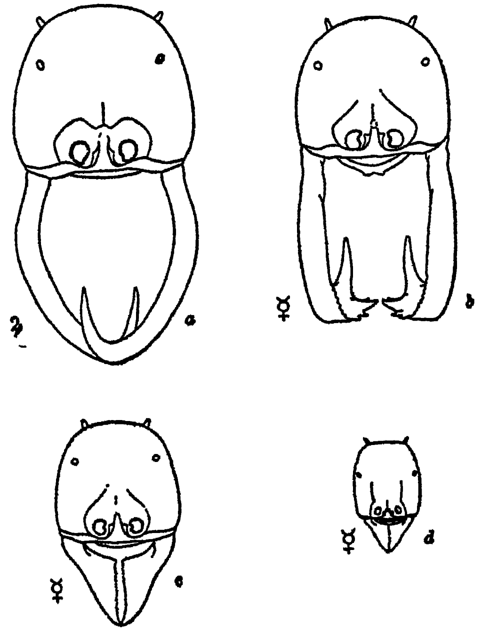

FIG. 25. HEADS OF A NEOTROPICAL ARMY OR LEGIONARY ANT (*Eciton burchelli* WESTW.)
a, soldier; *b*, form intermediate between soldier and worker; *c*, large, *d*, small worker.

In conformity with this unique behavior, the musculature of the mandibles

is peculiarly modified. The flexor mandibulæ (*fl.m.*) is very long and fills out the whole elongated posterior portion of the cranium. The tendon (*t*), attached to the swollen internal mandibular hinge, is expanded behind near the eye into a twisted, somewhat crescentic, chitinous plate (*t.pl.*) from which two long slender tendons run back very nearly to the posterior border of the head. Only one of these tendons is shown in the figure, because the other, which runs mesially and ventrally is concealed. The muscle-fibres are numerous, very short and attached to the tendons like the barbs of a feather to

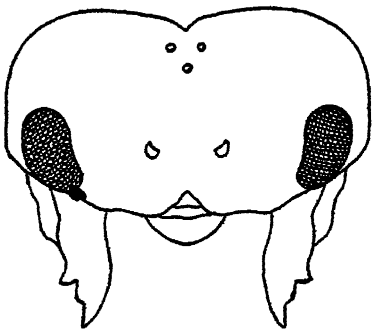

FIG. 26. HEAD OF *Alysia manducator* PANZ. OF EUROPE
Note the great width of the head, presumably to accommodate the *extensor* muscles of the mandibles, and the teeth on the *external* borders of the latter.

its shaft, but in three dimensions of space. In the neighborhood of the eye fibres also run from the crescentic chitinous plate to the anterolateral walls of the cranium. Since short muscle-fibres can contract more quickly than long ones, the whole arrangement seems to be beautifully suited to closing the jaws with much greater velocity than in other ants. And the large size of the flexor muscle as a whole shows that closure is effected with considerable vigor.

The mandibles of Dacetonine ants show a bewildering variety of forms, often much like those of *Odontomachus*. Some of the species are also able to leap backward. The head, however, has a very different shape (figs. 13 and 15). It is usually more or less cordate in the worker and female, with very prominent occipital lobes and these are filled with the huge flexor mandibulæ muscles. Their fibres, in some of the species at least, are arranged along the sides of a long tendon (fig. 13). Unfortunately we possess no information in regard to the feeding habits of these ants. If we may judge from their faces they certainly do not spend their lives diffusing sweetness and light. The heads of the male Dacetonini are extraordinarily different, as will be seen from the figure of the South American *Daceton armigerum* (fig. 17). The two large drawings (*a* and *c*) represent the heads of the female and worker, the small one the head of the male (*b*). Notice the vestigial condition of the mandibles, the shortness of the cranium and the complete suppression of the great lobes which in the other castes contain the flexor muscles of the mandibles. Owing to these deficiencies the countenance of the male wears a very meek and vacuous expression compared with the satanic countenances of the female phases.

Among the ants with aberrant types of mandibles I will select only two. In one of them, *Thaumatomyrmex* (fig. 19), of which only a couple of tropical American species are known, each mandible is split into three long slender spines. The narrowing and rounding of the posterior portion of the head indicates that the flexor muscles must be very feeble. We know nothing of the habits of these insects, only a few, isolated specimens of which have ever been taken. Perhaps they feed on very soft-bodied larvæ or small snails in which case the mandibles might be used for puncturing the integument of the prey in several places. The other type is that of *Harpegnathos*, an

East Indian ant with extraordinary mandibles known to be employed in leaping (fig. 20). The insect apparently bends its head completely under the body, presses the tips of the mandibles against the ground and by suddenly raising its head, leaps forward to a distance of a yard or more. This habit, however, does not completely account for the unusual conformation of the mandibular blades, especially of their large basal teeth (Wheeler, 1922).

Much of what I have said about the mandibles of ants, their musculature and the shape of the head will, I believe, hold good of many other mandibulate insects. Professor C. T. Brues, however, calls my attention to two unrelated groups of Parasitic Hymenoptera, the Alysiidæ and Vanhorniidæ, in which the function of the mandibles and probably also the development of their musculature are reversed. In the accompanying outline figure of the head of *Alysia manducator* (fig. 26) it will be observed that the mandibles have the teeth on their external instead of their internal borders. Obviously in this case the extensor muscles have much more work to perform than the flexors and are therefore probably larger. This is indicated by the unusual width of the head and the distance between the eyes. Of course, such exodont mandibles cannot be used for biting or mastication, but might be employed by the insect in forcing its way through soft wood, mushroom-tissues, etc. We unfortunately possess no observations on the habits of the Alysiidæ beyond the fact that their larvæ live in the larvæ of various Diptera, Coleoptera and Lepidoptera.

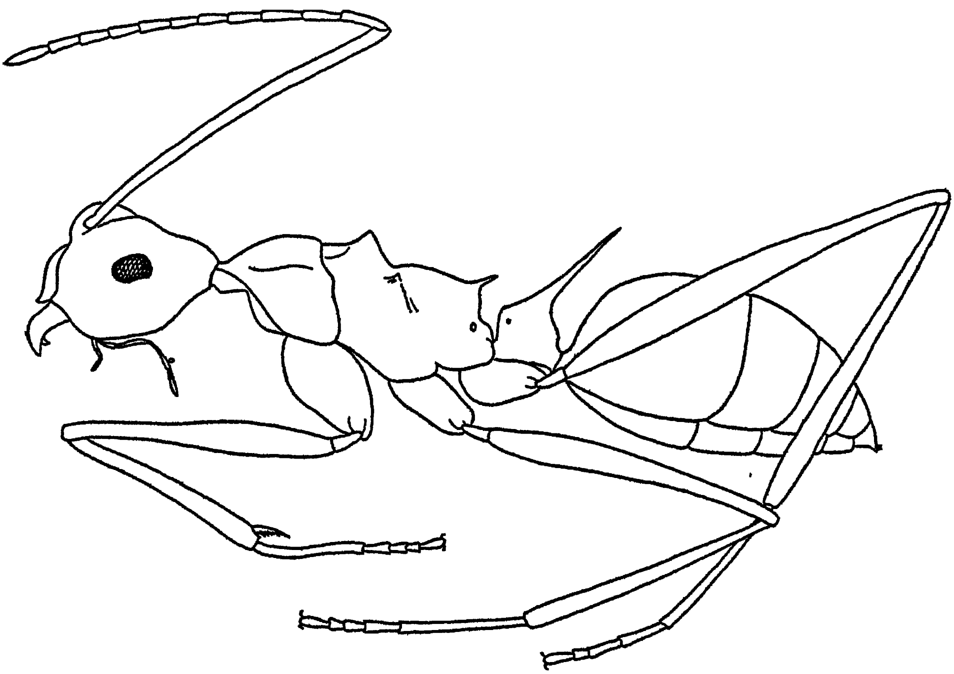

FIG. 27. *Polyrhachis (Myrmatopa) ulysses* FOREL FROM THE SOLOMON ISLANDS; WORKER IN PROFILE, SHOWING CONVEXITY OF THE FRONT

The heads of ants vary considerably in the convexity of their dorsal surface. As a rule, they are most convex in the region

of the vertex and occiput, a condition which is, of course, correlated with the development of the flexores mandibulæ already described, but in a few genera due to the greater development of the flexor and extensor antennal muscles, which run from the articulations of the appendages downward, backward and

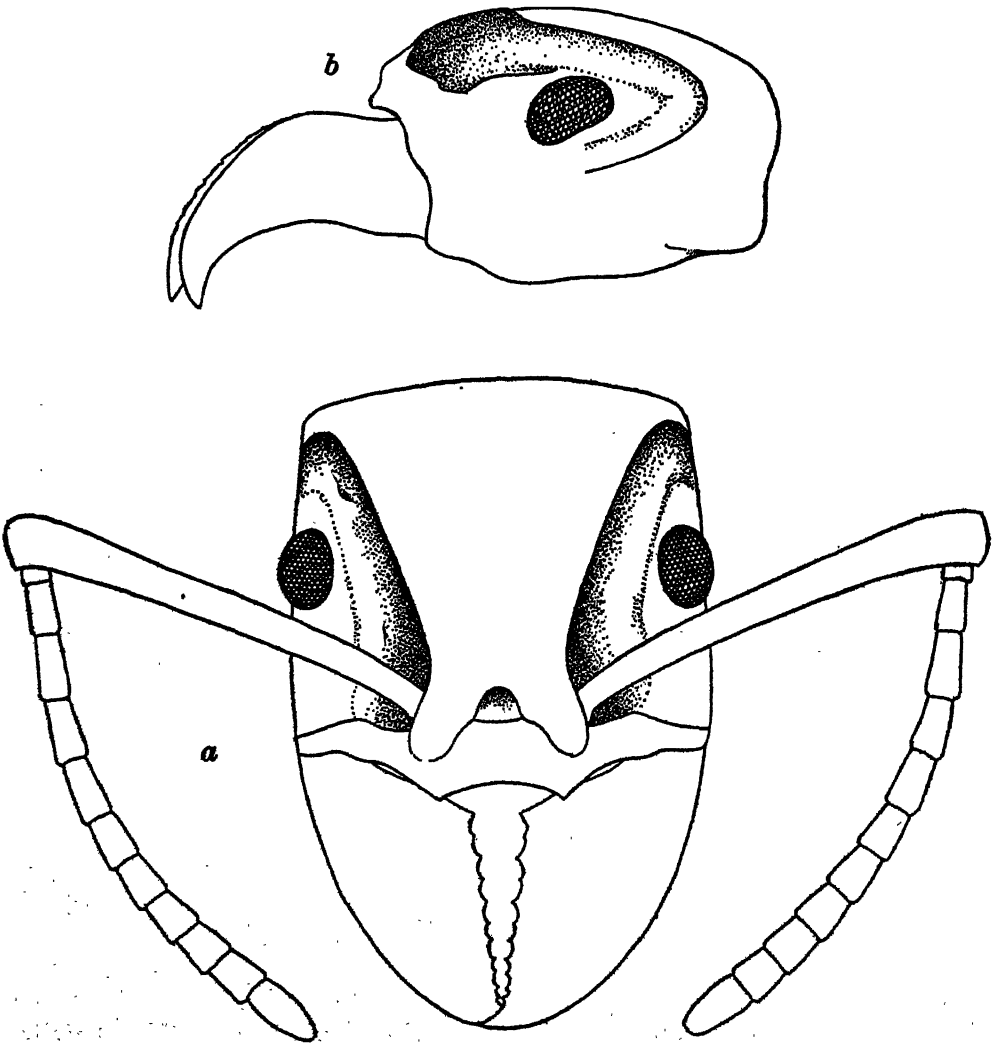

FIG. 28. HEAD OF THE FORMIDABLE "TUCANDEIRA" ANT, *Paraponera clavata* FABR., OF TROPICAL AMERICA, SHOWING THE PECULIAR ANGULATE SCROBE
a, seen from above; *b*, in profile

and notably in *Polyrhachis* (fig. 27) the front is conspicuously convex or protuberant. Since the antennæ are always long and very mobile in such insects I believe that the frontal convexity must be outward and are inserted on the limbs of the tentorium. I advance this merely as a suggestion, because I have not yet had an opportunity to study the anatomy of *Polyrhachis*.

DEVELOPMENT OF GROOVES FOR ANTENNÆ

The sides of the head in ants are sometimes peculiarly modified by the development of grooves, or scrobes for the partial or complete concealment of the antennæ. In their simplest form, e.g. in many species of *Pheidole*, *Harpagoxenus* and *Tetramorium*, these scrobes are formed by a backward prolongation of the frontal carinæ and a longitudinal depression of the adjacent cranial surfaces. In certain other genera, however, the grooves become deeper. In *Paraponera* (fig. 28) we find a very peculiar scrobe with two limbs forming an angle around the eye. At first sight this structure would seem to be an adaptation for receiving both the scape and the flagellum of the antenna, but the scape and flagellum are really too long to form an angle that will fit into the scrobe. Hence the dorsal limb can accommodate only the basal portion of the scape when it is folded back and the ventral limb only the tip of the flagellum. In *Paranomopone* the scrobe is divided near the middle by a slender partition into two grooves one of which accommodates the scape, the other the flagellum. In still other genera the scrobe is simple but sufficiently deep to receive the whole folded antenna or at any rate the whole scape (fig. 29). In *Cryptocerus* (*a*) the scrobe lies in front of the eye, in *Procryptocerus* and *Meranoplus* (*b* and *c*) it runs backward over the eye, in *Cataulacus* (*d*) it descends below the eye. In all of these genera, and especially in *Cryptocerus*, the frontal carinæ may be greatly expanded laterally, so that the head becomes very broad and shield-shaped, with plate-like lateral margins (fig. 30).

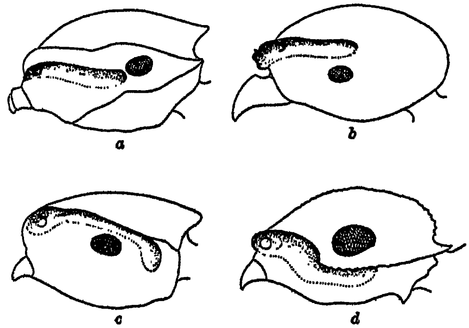

FIG. 29. PROFILES OF HEADS OF VARIOUS ANTS TO SHOW DEVELOPMENT OF THE ANTENNAL SCROBE AND ITS RELATION TO THE EYE

a, *Cryptocerus multispinus* Sm.; *b*, *Meranoplus mars* Forel; *c*, *Procryptocerus belti* Forel; *d*, *Cataulacus erinaceus* Stitz

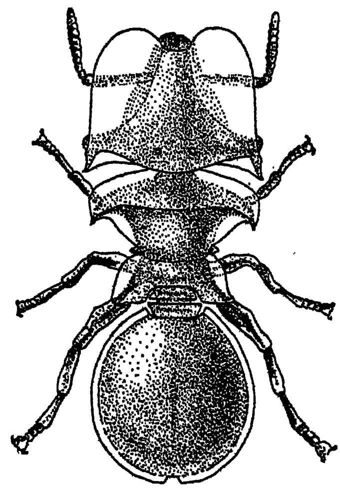

FIG. 30. *Cryptocerus* (*Zacryptocerus*) *clypeatus* F.; WORKER, WITH THE HEAD BROADENED AND FLATTENED FOR USE IN PHRAGMOSIS

(After C. Emery)

The scrobes suggest an interesting evolutionary problem. It would seem that they might be formed in the pupa by the pressure of the antennæ against the still soft and plastic cranial integument, but when we examine the young pupæ of the various genera I have mentioned, we find that the antennæ are not folded up against the sides of the head but are drawn down over the ventral surface of the legs as in the pupæ of many other insects. The scrobes therefore develop independently during the ontogeny and we are compelled to conclude that

these grooves, so beautifully adapted in the adult to the reception and protection of the very sensitive and important antennæ, must have arisen during the phylogeny of the various species in which they occur. The notion that they were produced by natural selection may be dismissed as improbable for the simple reason that they cannot have had survival value, because they are altogether lacking in most of the larger and more dominant genera (*Monomorium*, *Crematogaster*, *Polyrhachis*, *Formica*, most *Camponotus*, etc.). The only hypotheses, it seems to me, that might be advanced to account for the scrobes are those that have been discussed in connection with many similar cases of functionally correlated structures, namely, first, the Lamarckian hypothesis that habitual pressure of the antennæ against the hard integument of the adult cranium has affected the germplasm in such a manner as to lead to the gradual development of scrobes in the pupal offspring of succeeding generations, and second, the mutation hypothesis of the chance, spontaneous origin of scrobe-producing genes in the germplasm. The latter hypothesis fails to account for the highly adaptive character of the scrobes and the former labors, of course, under the difficulty of explaining how the habitual pressure of the antennæ against the hard, unyielding cranial cuticula of the adult could translate itself into a definite formative, or morphogenic tendency in the individuals of succeeding generations.

PROBLEMS OF ADAPTATION

A number of exquisite structures similar to those here described have been discussed by Cuénot (1925) in his very interesting little book on adaptation under the head of "coaptations." These he defines as "reciprocal adjustments of two independent parts analogous to that formed by the blade fitting into the handle-groove of a pocket-knife, or a button into its button-hole." As examples he cites the fore legs of certain Phasmids which are curiously bent at the bases of the femora to fit around the head, a case originally described by Stockard (1909), the pressure-button (used on gloves and invented in France about 1886), shown in the two attachments of the mantle in cuttle-fishes and the attachment of the hemielytra to the thorax in numerous aquatic Hemiptera, or Hydrocorisa (*Ranatra*, *Belostoma*, *Notonecta*, *Naucoris*, etc.), the devices in many insects for attaching or fitting the wings or elytra to one another, the coaptation of the blades of the ovipositor in Orthoptera, the stridulatory apparatus of Elaterids and other insects and the raptorial fore legs of numerous bugs, Mantids, Mantispids, scorpions and crustaceans. To this list we may add the Hymenopteran strigil which is formed by the spur of the tibia and basitarsus. After excluding the origin of such structures by mutation, and omitting all mention of the Lamarckian hypothesis, Cuénot says:

> Without a doubt, coaptation is the end-stage of a *directed* evolution. Sufficient indications of this evolution are known to permit its affirmation. There are Phasganourids with short ovipositors which have gutters that are rather imperfect though adequate for the movements of oviposition. There are, foreshadowing the saltatory apparatus of Elaterids, certain imperfect conformations of a similar type; the *Corisas* have an apparatus simpler and less compact than the pressure-button of other aquatic Hemiptera, many predatory insects have ambulatory legs which serve equally well for seizing the prey though not of the highly differentiated type of the specialized raptorial legs in the Mantids and Naucorids. Now the only directing agency we know is Darwinian selection. This would have to play the rôle of a handicraftsman gradually correcting and perfecting his work, successively and tentatively, till it attained a complete and definitive functional specialization which could not be surpassed. Even admitting the omnipotence of natural selection, however, it could

not create the coordinated details of the coaptations, and it is just the origin of these details we find so difficult to understand And then how improbable it is that the elytral apparatus of a *Lucanus*, the spur of the raptorial legs of a *Ranatra*, the stridulatory rasp of a longicorn, can have had sufficient vital importance during their incipient stages to have brought about differential extinction! But after these negations, nothing remains It would be pure metaphysical amusement to imagine within the species a meticulous and fanciful demon, a regulator and director of mutations, even if he were decorated, as he has been by some, with such pompous epithets as 'internal perfective tendency,' 'élan vital,' 'entelechy,' or some other term Again we must resign ourselves to saying *ignoramus*!

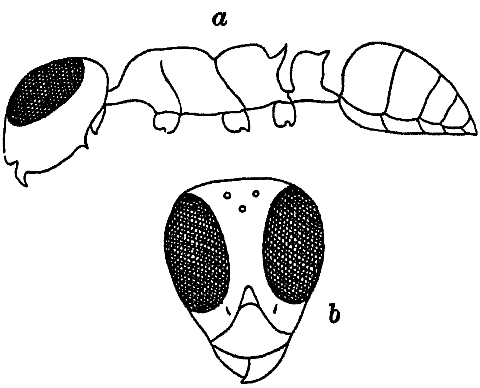

FIG 31 *Santschiella kohli* FOREL, A HUGE-EYED FORMICINE ANT FROM THE CONGO

a, worker in profile, *b*, head of same from above (After Forel)

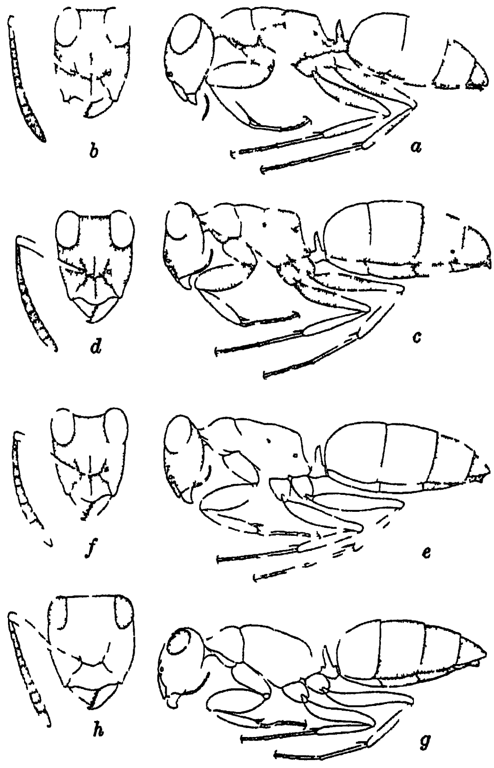

FIG 32 WORKERS OF FOUR SPECIES OF THE LARGE-EYED AUSTRALIAN GENUS *Opisthopsis*

a and *b*, *O respiciens* Sm , *c* and *d*, *O pictus* Emery var *lepidus* Wheeler, *e* and *f*, *O rufithorax* Emery, *g* and *h*, *O major* Forel

DEVELOPMENT OF EYES

Much might be said about the physiognomic significance of the eyes of ants and other insects, but the space allotted to this article and the reader's patience are limited, and I must be brief. In nearly all male Formicidæ, of course, the eyes are very large, but this is true of the females and workers only in a few rather primitive and archaic genera. The facial expression of these macrophthalmic forms is very unlike that of other ants. Thus *Santschiella* (fig. 31), which is known only from a single worker specimen taken in the Belgian Congo looks as if it were

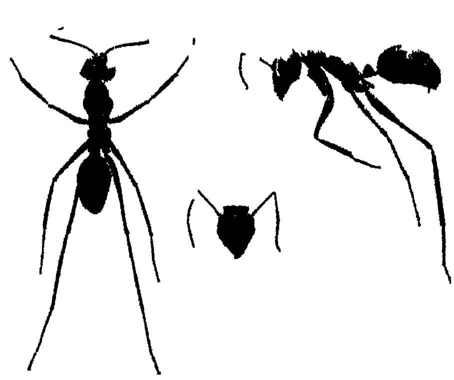

FIG. 33. A LARGE-EYED LEAPING ANT, *Gigantiops destructor* FROM BRITISH GUIANA

Dorsal and lateral view of worker and head seen from above

hopelessly flabbergasted by the problem of existence and therefore resigned to race-suicide, and the species of the Australian genus *Opisthopsis* (fig. 32) and the neotropical *Gigantiops* (fig. 33), which have the large eyes at the posterior corners of the head, wear the expression of pained astonishment which as children we have all seen on the face of some school-marm or elderly maiden relative. It is more difficult to characterize the expression of the East Indian *Myrmoteras* (fig. 14) with its unique combination of huge eyes and clipping mandibles. If there are Anthony Comstocks, movie censors and prohibition agents among the ants we might, perhaps, expect them to have just such faces.

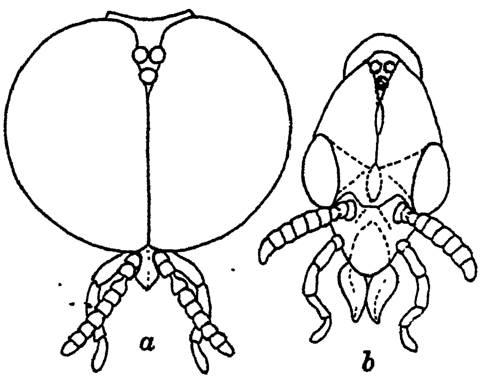

FIG. 34. *Bibio hortulanus* L., A EUROPEAN DIPTERON *a*, head of male; *b*, head of female. (After Berlese)

Large as are the eyes in these various ants they are not nearly as well-developed as those of many other insects, like the Diptera, Lepidoptera, Odonata, many Hemiptera, etc. In most of these orders, however, the mandibles are poorly developed or reduced to stylet-like appendages. In many male Diptera the eyes form nearly the whole head. An instructive case is furnished by *Bibio* (fig. 34) in which this condition is seen in the male, while the female has very small eyes and a very different head, narrowed and rounded behind like that of certain ants (*Lobopelta*) with poorly developed mandibles.

BEARDED ANTS

Of course, the physiognomy of ants is also determined to some extent by the character of the sculpture and pilosity. The sculpture, especially when it assumes the form of rugæ or reticulations is sometimes strangely suggestive of the wrinkles in the aged human countenance (*Diacamma*, some species of *Pheidole*, etc.). The various coiffures and styles of moustaches, whiskers and eyebrows are often extraordinary, but I will not dwell on them, because I might be tempted to depart too far from the arctic dignity so becoming to an entomologist. Nevertheless there is one type of beard to which I must call attention, because it has a very precise and practical function, unlike the human beard, which is supposed to have a great variety of functions—aesthetic, honorific, bacteriologic (or rather bacteriolegic), camouflagic, calorific, or merely problematic. And whereas in the human species it is the peculiar prerogative of the male to wear this form of pilosity, among the ants it is—*horribile dictu*—the females, i.e., the queens and workers that insist on cultivating it. But such improper customs prevail only among the species that live in deserts. Some years ago I discussed these ants in a tonsorial paper which might have attracted more attention had it been published in some barber's monthly instead of the Biological Bulletin (Wheeler, 1907).

Among the dominant ants of the arid, desert regions of the globe there are a number of species belonging to several genera and no less than three of the seven natural subfamilies (Myrmicinæ, Dolichoderinæ and Formicinæ) which have

series of conspicuously long, curved hairs on the chin (gula), mandibles, and clypeus (fig. 35). The arrangement of these hairs which form a kind of crate is most typical and most like that of the old-fashioned Irishman's chin-whiskers in the large Western harvesting ants of the genera *Pogonomyrmex* (fig. 35*a*) and *Veramessor*, and of the genus *Messor*, which ranges over the dryer parts of Africa,

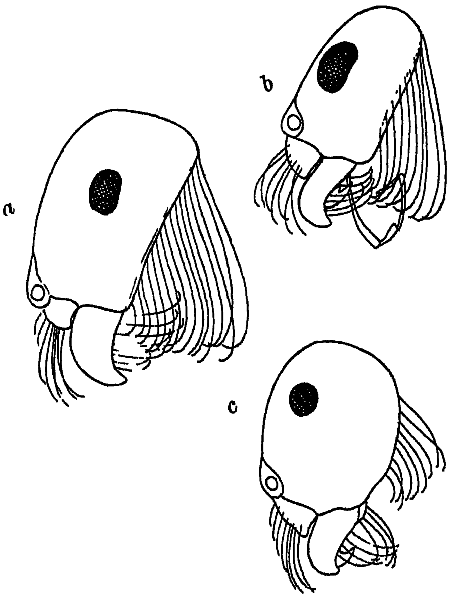

FIG. 35. HEADS OF DESERTICOLOUS ANTS IN PROFILE TO SHOW DEVELOPMENT OF THE PSAMMOPHORE IN THREE DIFFERENT SUBFAMILIES

a, *Pogonomyrmex californicus* from Southern California (Myrmicine); *b*, *Dorymyrmex* (*Psammomyrma*) *planidens* from Argentina (Dolichoderine); *c*, *Melophorus bagoti* from Central Australia (Formicine).

southern Europe, and Central Asia. Similar hairs are also developed in the deserticolous species of *Monomorium*, *Dorymyrmex* (fig. 35*b*), *Melophorus* (fig. 35*c*), *Cataglyphis*, *Myrmecocystus*, and *Camponotus*. Santschi (1909) has shown that the gular crate, which he calls the "psammophore," is used as a basket in which to carry the sand and dust to the surface while the insects are excavating their burrows. Without such equipment the species nesting in dry sand or earth would probably find excavation extremely laborious and time-consuming, because the mandibles are not suited to the transportation of very finely-divided or powdery substances.

Besides the psammophore just described there are in certain ants other more important modifications of the head that may be interpreted as adaptations to the non-living environment. The most conspicuous of these have evidently developed in response to the habitual contacts of the insects with the walls of their burrows, especially when they are tubular and excavated in solid wood. Similar and even more striking cases are well-known among both larval and adult beetles, notably among the Ipidæ, Platypodidæ, Bostrichidæ, Ptindæ, Cerambycidæ, etc. The insect, especially if it rotates while boring through the wood, makes a perfectly tubular gallery, in adaptation to which the body takes on a more or less perfectly cylindrical form. But since most ants, even many of the wood-boring species, have rather long, slender bodies, they need to acquire no special adaptive change in structure, though in some tropical species, and especially in the queens, the tenuity of the body may be greatly exaggerated. This is the case, e.g., in the Myrmicine *Pseudomyrma filiformis* (fig. 36) which, according to my observations, regularly inhabits the very narrow pith-cavities of a particular neotropical shrub. And in *Camponotus* (*Myrmostenus*) *mirabilis* (fig. 37) which belongs to a different subfamily, the Formicinæ, we find a very similar elongation of the head and body. The latter species is known only from single female specimens taken at lights, but there can be little doubt that its nesting habits are much like those of *Ps. filiformis*.

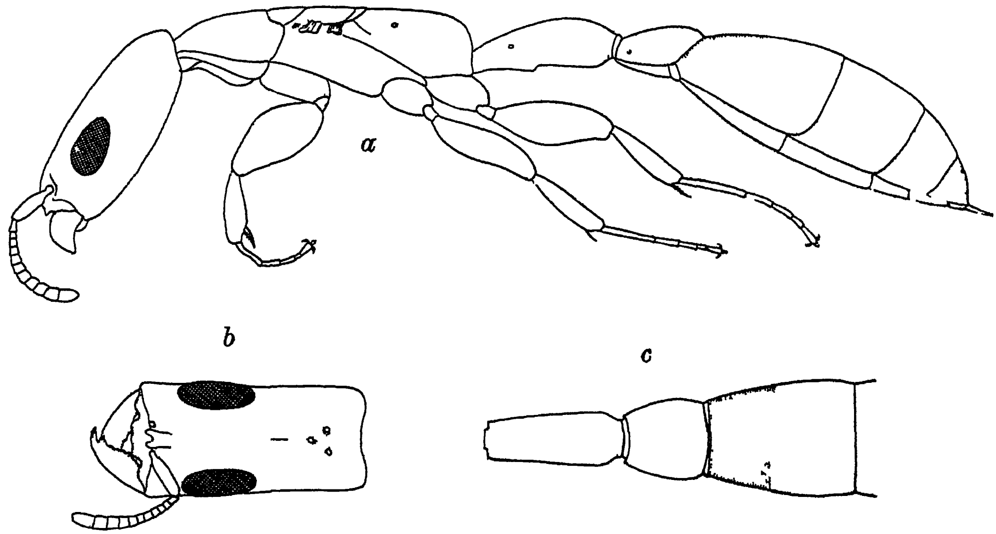

FIG 36 A NEOTROPICAL PSEUDOMYRMINE ANT, *Pseudomyrma filiformis* FABR, ADAPTED TO LIVING IN HOLLOW TWIGS

a, female (dealated) in profile, *b*, head of same from above, *c*, pedicel and first gastric segment from above

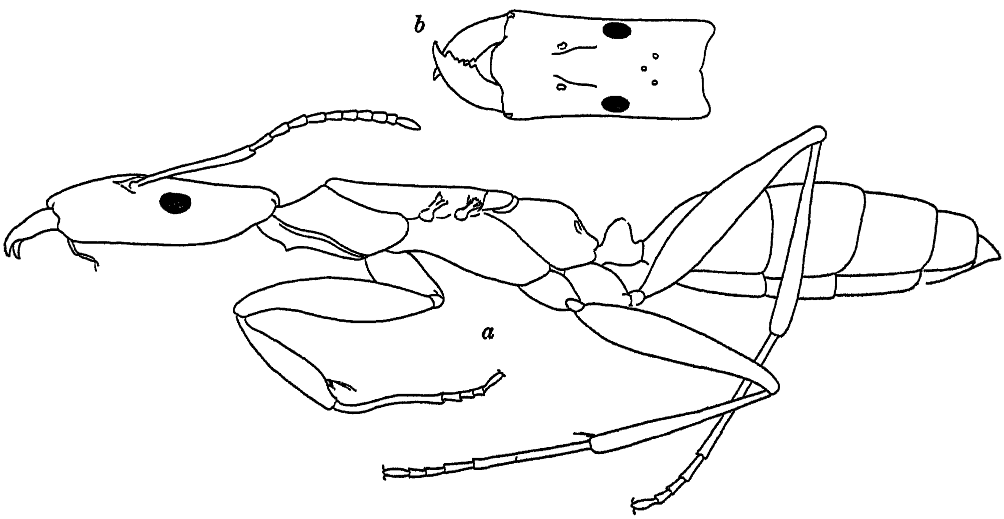

FIG 37 *a*, FEMALE (DEALATED) OF A PERUVIAN FORMICINE ANT, *Camponotus* (*Myrmostenus*) *mirabilis* EMERY, ADAPTED TO LIFE IN HOLLOW TWIGS, *b*, HEAD OF SAME FROM ABOVE

PHRAGMOSIS

A more interesting adaptation to living in hard-walled, tubular cavities occurs in several genera, e g , *Camponotus*, whose queens and soldiers have short, cylindrical and anteriorly sharply truncated heads, with the truncated surface circular, indurated and more strongly sculptured than the remainder of the body (fig. 38) These ants use the head, like the thick door of a safe, to close the entrance of the nest and keep out intruders The nest which is excavated in hard wood, lig-

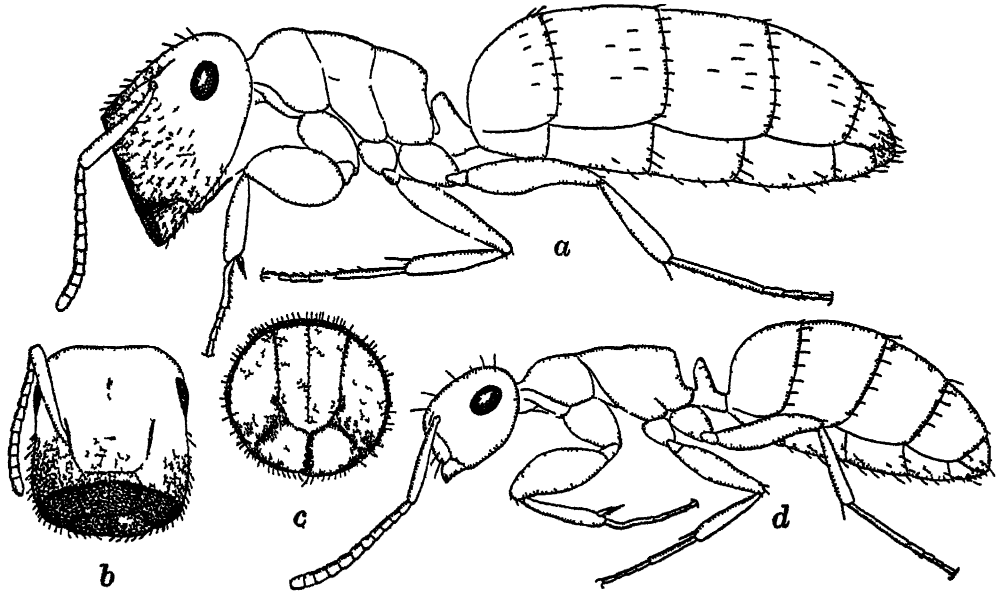

FIG 38 *Camponotus (Colobopsis) etiolatus* WHEELER, A COMMON PHRAGMOTIC ANT IN THE LIVE OAK GALLS OF TEXAS

a, soldier *b*, head of soldier from above, *c*, same directly from front, *d*, worker

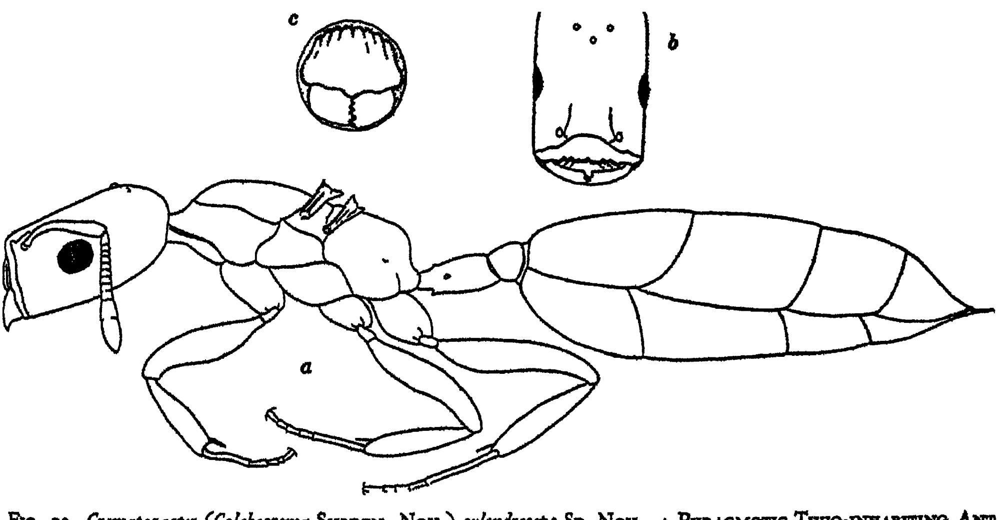

FIG 39 *Crematogaster (Colobocrema* SUBGEN NOV) *cylindriceps* SP NOV , A PHRAGMOTIC TWIG-INHABITING ANT FROM THE PHILIPPINES

a, female (dealated) in profile, *b*, head from above, *c*, anterior view of head

neous galls or the stems of rushes, has a perfectly circular entrance which is guarded by a soldier whose head exactly fits the orifice. When a worker desires to forage she strokes the soldier's abdomen with her antennæ and the animated door moves back and as soon as she has passed out of the nest returns at

once to its previous position. On returning she knocks with her antennæ on the exposed truncated surface of the janitor's head and a similar response permits her to enter. I find this same type of head in single exotic species of three other unrelated genera: *Pheidole*, *Crematogaster* (fig. 39), and *Epopostruma* (fig. 40), which, in all probability have much the same habits. There are also several lignicolous subgenera of *Camponotus* (*Paracolobopsis*, *Pseudocolobopsis*, *Manniella*, *Neomyrmamblys*) which exhibit similar modifications of the head in the queens and major workers. In some species of *Cryptocerus*, which also live in hard wood, the heads of the soldiers are broad and shield-shaped, and are also used for closing the nest-entrances.

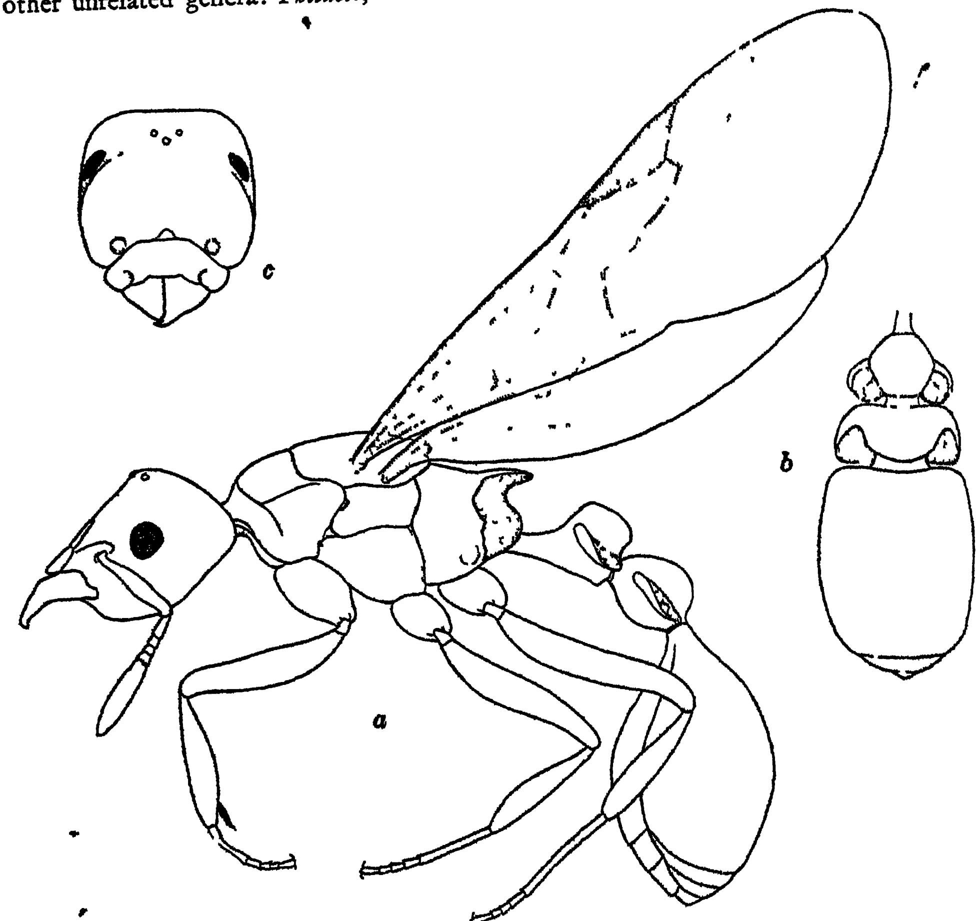

FIG. 40. *Epopostruma* (*Colobostruma* SUBGEN. NOV.) *lea* SP NOV., A PHRAGMOTIC ANT FROM AUSTRALIA
a, female in profile, *b*, pedicel and gaster, *c*, head from above

The peculiar plug-like modification of the ant's head, like the scrobes, suggests an interesting problem which can be briefly discussed in this place. Very similar adaptations for closing the entrances to the burrows are found not only in a number of other Arthropods (e.g., in the termites of the genus *Cryptotermes*) but also in animals belonging to other phyla.

In some cases the head, in others the posterior end of the body is adaptively modified, but in both instances the truncation, its circular outline and the hardening of its integument are strangely similar Sometimes, as in the larvæ of tiger-beetles (*Cicindela*) and the burrowing bees of the genus *Halictus*, the whole head is nearly

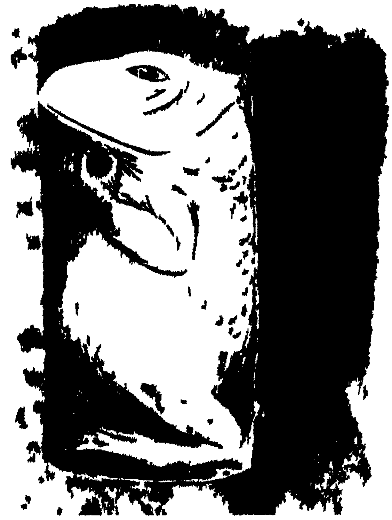

FIG 41 A TOAD, *Bufo empusus* FROM CUBA, WHICH CLOSES ITS EARTHEN BURROW WITH ITS HARD, SHELLY HEAD
(After T Barbour)

circular and plug-shaped, in other forms, like the bark-beetles (Scolytidæ, Platypodidæ) and the caterpillars of *Circinnus melshaemeri* and *Perophora sanguinolenta* which inhabit tubular cases made of leaves, the posterior end of the body is sharply truncated and roughened or spinulate A figure and description of the habits of *C melshaemeri* is given in Harris (1862), while *P sanguinolenta* is figured in Sharp (1899). I have observed the caterpillars of the latter or an allied species in British Guiana In certain Annelids (Maldanidæ, Amphictenidæ) that live in tubular burrows, the head is hard and shelly I reproduce Petrunkevitch's figure of a peculiar Theraphosid spider (*Chorizops loricatus*) (fig 42) which, instead of making a trap-door like the allied species, uses the posterior end of its body for closing its burrow

Barbour (1914, 1919, 1926) and Dunn (1926) have recently called attention to several interesting cases of the closure of burrows with modified heads and posterior ends in vertebrates Barbour in his delightful book on reptiles and amphibians says ' It is well known that in many frogs the skin of the head becomes involved in the cranial ossification and becomes adherent, indurated, and rugose ' This makes a hard bony head and should the frog back into a burrow it has but to tip his head down to close the entrance effectively. That this was ever regularly done on a large scale was never known until by chance, the author, after many long hunts for *Bufo empusus* in Cuba, chanced upon an open field over which were scattered many small burrows These were evidently of two sorts, for the openings of some were carefully rimmed with smooth patted clay, while the others were rough and looked unfinished Each of those with the rims contained one of the toads for which he had searched so long—the *sapo de concha* in Spanish—the shell-headed toad These tube-like burrows were perfectly cylindrical, and perhaps seven to ten inches deep The toad, which always looked larger than the burrow, when it was removed, was to be found near the bottom of the hole, the horn-like head forming a perfect operculum and perfectly fitting the caliber of the

tube." With Dr. Barbour's permission I reproduce his figure of this toad (fig. 41). Both he and Dunn have shown that a very similar closure of the burrow occurs in a number of wood inhabiting tree-frogs (e.g. in *Hyla lichenata* of Jamaica). In this connection Barbour also calls attention to two other groups of vertebrates in which the posterior end of the body is similarly employed, namely the snakes of the family Uropeltidæ, "where the head is sharp and the tail knobbed and shielded off and is covered by a bony shield. This closes the burrow perfectly and no prying snake following its underground path could possibly get its jaws about it."

As there is no general term to cover all the peculiar, sporadic but convergent modifications of the ends of the body for closing tubular burrows I suggest the word "phragmosis," from φραγμός, a fence or barricade. From evolutionary and behavioristic points of view the phenomenon, as one of the most striking and

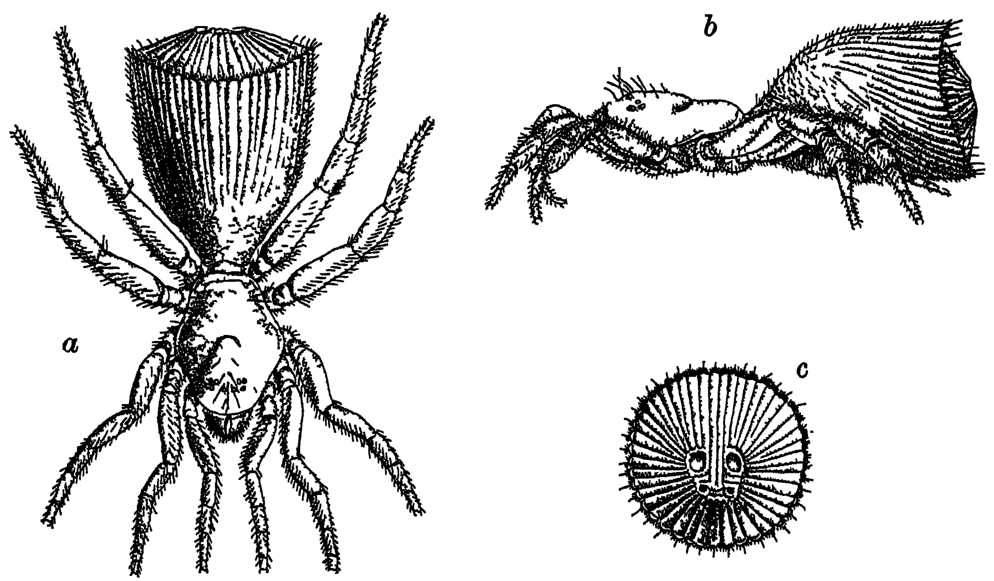

FIG 42. A NEOTROPICAL SPIDER (*Chorizops loricatus*) WHICH CLOSES ITS BURROW WITH THE TRUNCATED POSTERIOR END OF ITS ABDOMEN

a, dorsal view, *b*, lateral view, *c*, truncated surface of abdomen. (After A. Petrunkevitch)

or even sometimes roughened," and certain small armadillos, of which he says: "Perhaps the most marvelous example of all is to be seen among mammals, in the two species of Pichiciegos of Bolivia and northwestern Argentine. These little armadillos of the genus Chlamydophorus burrow and live underground. Their body is nearly cylindrical, the head sharp and pointed, and the great fore limbs are mole-like in the extreme, but the posterior end of the body is as if sharply chopped

definite methods of protection and defence, would seem to deserve more careful investigation than it has received. The phragmotic insect, instead of secreting or constructing a stopper, like the operculum or epiphragm of snails and the earthen or silken barricades or doors erected at the entrances of their burrows by many ants, wasps and trap-door spiders, actually employs for the purpose a specialized portion of its own body, thus affording a proof that no hard and fast line can be drawn

between behavioristic activities on the one hand and physiological and morphogenic processes on the other. The phylogenetic development of phragmosis is obscure. The ants, at least, seem to indicate that it cannot have arisen as a sudden, saltatory variation, but must have developed gradually, since we have among the many species of lignicolous *Camponoti* continuous series of approximations to the perfected condition observed in *Colobopsis* (fig. 38).

DETERMINATION OF SHAPE OF THORAX AND ABDOMEN

It will be seen from the foregoing discussion that the most important general factor in determining the shape and size of the head, at any rate in insects with biting mouthparts, is the flexor musculature of the mandibles. When we turn to the great motor region of the insect body, the thorax, the dependence of the size and shape of the skeleton on the volume of the leg and especially of the wing musculature, becomes even more manifest. Attention has been so often directed to this matter, that little remains to be said about it. Such insects as the aphids show the correlation very clearly during their post-embryonic instars, but the various castes even of a single species of ant, furnish an even more impressive illustration. In worker ants, which never develop wings, save as rare, pathological vestiges, the thorax is greatly simplified in structure and diminished in size as compared with the thorax of the winged castes; and among the queens of certain species (*Leptothorax emersoni*) we discern a gradual reduction in its size and complexity as we pass from the macrothoracic, winged individuals, through steno- to microthoracic, apterous forms essentially like the workers. That the development of the wing-muscles very largely determines the size and shape of the thorax is also revealed by a comparative study of insects like the Odonata, Hymenoptera, Diptera and Coleoptera, in which the relative volumes of the meso- and metathoracic segments are clearly correlated with the relative size and efficiency of their respective pairs of wings.

The physiognomy of the insect abdomen, however, is not determined so much by the development of the musculature of the various segments as by the volume of the viscera, i.e., the alimentary canal, reproductive organs and fat-body. The phenomenon of "physogastry," or hypertrophy of the abdomen is in some cases due to an enormous increase in the contents of the crop, as in the honey-ants, in others to enlargement of the ovaries or fat-body, as in the aged queens of termites and certain ants (*Dorylinæ*, *Anergates*) and the various termitophiles of the more extreme type (*Corotoca*, *Spirachtha*, etc.). This physogastry is really of considerable physiological interest but its adequate consideration would unduly expand this article.

In conclusion we may revert briefly to some of the general types observed in man—the dysplastics, giants, dwarfs and acromegalics. Stockard has shown that very similar types may be clearly recognized among the various breeds of dogs, such as the St. Bernard (acromegalic), bull-dog (achondroplastic dwarf), black-and-tan (ateleotic dwarf), etc. Many cases of giantism and nanism might be cited among the insects, and among the dwarfs the soldiers of certain ants (*Pheidole*, *Acanthomyrmex*, etc.) are in many respects strangely analogous to the achondroplastics (fig. 21*a*), while the small workers (fig. 21*f*) are even more like the ateleotics. The development of these forms evidently depends on both genetic

and endocrine factors but the proportional intervention and interrelation of these factors have not been established. Owing to lack of knowledge of the precise functions of the various glands which in insects might be regarded as analogous to the endocrine glands of vertebrates, we are unable to frame any satisfactory physiological explanation of the Hexapod dwarfs. If certain ants have really learned to produce achondroplastics and ateleotics *ad libitum* and to turn over to them the main asexual activities of the colony, we should have another fine example of the extraordinary ability of insects to exploit to the utmost everything in their environment. As yet man has learned to employ his achondroplastics, ateleotics and other dysplastics only as court pets, court jesters and circus freaks.

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ANTHROPOID BEHAVIOR

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INTRODUCTION

IN THE first quarter of the present century both scientific and popular interest in the anthropoid apes has increased steadily and greatly. Publications have multiplied correspondingly. Despite lively interest in other primates, and in other phenomena than those of behavior, we have been constrained by the magnitude of our task and the space allotted us to limit this digest to studies of the behavior and mentality of the four existing types of anthropoid ape: the gibbon, the orang-utan, the chimpanzee, and the gorilla. For convenience we shall hereafter use the term ape as synonymous with anthropoid ape.

Morphologic, taxonomic, and physiologic publications, however intimately related to psycho-biological problems, have been omitted unless they contain significant original contributions to behavior. As our primary recent sources of aid in matters of classification, structure, and genetic relations, we have used the pertinent works of Elliot (28) and Sonntag (72). The former, in addition to taxonomic information, supplies an immense amount of miscellaneous material on the habits and life-history of the apes, and the latter, with his convenient summary of their morphological characteristics, supplies a bibliography of over five hundred titles. Although many authors consider anthropoid characters, discussions of evolution have been omitted from this digest because they give but scant and inexpert attention to psycho-biological phenomena.

The chronological limits of our survey were dictated by the beginnings in 1912 of determined endeavor to provide facilities for anthropoid research, and by the date of writing—March, 1926. Prior to 1912 no major experimental contribution to our knowledge of the behavior of an anthropoid ape had been published.

Although it necessitates slight repetition of references, topical arrangement of materials has been employed and generally under topics the chronological order. Popular papers have been ignored, except in those few instances in which they present original observations. Ordinarily, we have excluded also preliminary announcements, summaries, and abstracts. Aside from these intentional omissions the bibliographic list is thought to be reasonably complete.

HISTORY OF ATTEMPTS TO PROVIDE FOR ANTHROPOID RESEARCH

In 1912 appeared the first account of a plan for an anthropoid station on Tenerife, the Canary Islands. It originated apparently with Professors Rothmann and Waldeyer in Berlin (62, 63, 74, 75). Rothmann's publications fully describe the project. Dr. E. Teuber, a young German psychologist, was the first resident investigator. His period of residence was short and but one publication (64) reports his work. His successor,

Dr. W. Köhler, continued in residence at the station for several years conducting psycho-biological investigations. During the World War he was virtually interned on Tenerife and lacked scientific resources and contacts essential to the satisfactory conduct of his work. Following the war the Canary Island Anthropoid Station was discontinued because of lack of funds for its maintenance; Dr. Köhler returned to Germany, and the survivors among the chimpanzees which had served as his subjects were transferred to the Berlin Zoölogical Garden.

The German station was established primarily to afford opportunity for studies in structural and functional neurology, but the experimental work actually conducted there during the six or seven years of its existence was psycho-biological and concerned almost wholly with problems of anthropoid behavior. It is one of the major tragedies of biological science that this initial effort to make excellent provision for the scientific study of the apes should have failed from lack of funds.

Simultaneously with the fostering and expression of interest in anthropoid research in Berlin, similar interest gained expression in the United States in the activities of Hamilton in California and Yerkes in Harvard University. The former for several years maintained at Santa Barbara, California, a small colony of monkeys and apes in which he studied various psycho-physiological problems, with special reference to his professional interest in psychopathology. Subsequently, the Hamilton colony was used by Yerkes in an experimental study of ideational behavior. Both colony and laboratory were abandoned when during the World War Dr. Hamilton found it necessary to leave California.

Between 1920 and 1924 the Pasteur Institute developed plans for the establishment and use of an African anthropoid station in supplementation of its resources for medical research. The first published descriptions of the project are those of Calmette (20, 21), Director of the Pasteur Institute. It appears that in 1924 a station had been located at Kindia in French Guinea (Africa), ample grounds developed, and several buildings erected. Various medical inquiries have been in progress at Kindia since that date.

Beginning early in the century, Señora Rosalia Abreu gathered as pets on her beautiful estate in Havana a collection of monkeys and apes. Despite its relatively long existence this primate colony, recently utilized for studies in behavior by H. C. Bingham and Yerkes, and described by the latter in a semi-popular book (80), has only incidentally and to a disappointingly slight extent contributed to the solution of biological problems. At the date of writing, the Abreu colony is larger and more varied than ever in its history. Probably it is the most extensive and otherwise valuable collection of primates in existence.

On the assumption that a primate breeding station should be located in a tropical or subtropical climate and should be constituted the field and supply station of a well equipped, favorably located northern research institute or university, effort in America has been directed to the development of special provision for morphological, anthropological, physiological, sociological, and psychological study of the primates. With the organization of the Institute of Psychology at Yale University in 1924, arrangements were made for the use of anthropoid apes, and in the following year a special Primate Laboratory was established in New Haven. Thus far, chimpanzees only have been used in this laboratory. It has been

Courtesy of Mrs. Kohts

LADYGIN-KOHTS STUDYING VISUAL DISCRIMINATION IN THE CHIMPANZEE

found possible to keep them in good condition and to work satisfactorily with them. The logical development of this plan, which is an outgrowth of Yerkes' pre-war efforts to achieve adequate provision for the thorough and inclusive study of the anthropoid apes, involves such institutional and departmental coöperation of biologists as will assure the efficient utilization of anthropoid materials and the early establishment of a subtropical breeding and observation station.

For two or three years during the World War, Madam Ladygin-Kohts, Director of the Zoö-psychological Laboratory of the Darwinian Museum, Moscow, kept in her institution a young chimpanzee which she used for experimental studies of sensory discrimination and perception. It is not indicated in her publications (48, 49) that permanent provision has been made in Moscow for the maintenance or study of apes.

The representations of Carl Akeley (3, p. 248) interested the Belgian Government in the establishment of a large national park in the Belgian Congo to provide safe habitat for several African animals which are in danger of extermination. In the midst of this great reservation is a sanctuary for the mountain gorilla (*G. beringei*). It is proposed to build in this gorilla preserve quarters for scientific observers.

On the whole, the spread and intensification of interest in the anthropoids, and in the meagerness of our knowledge, are vastly more encouraging than the measure of progress in the last decade toward provision for wise utilization of these relatively rare and strategically important materials of biology.

GENERAL AND HISTORICAL ACCOUNTS OF ANTHROPOID BEHAVIOR

Excellent general accounts of the anthropoid apes and of the history of our knowledge of them are few, within the period of this digest, and exclusively German. By far the best semi-popular and authoritative book is the thirteenth volume of the fourth edition of Brehm's "Tierleben" (16). In this, the latest, edition of Brehm's great work, four volumes are devoted to the mammalia and of these the last volume includes the apes. The work is remarkable for readability, scope and reliability of information, and abundance and excellence of illustrations.

Under the editorship of Carl W. Neumann, a large part of the description of apes originally presented in the "Tierleben" has been reprinted in a pocket-sized volume (17). The editor has extended the work by drawing upon recent experimental studies of anthropoid behavior. This handy volume constitutes an almost ideally concise and convenient source of general information about the manlike apes for those who desire introductory acquaintance rather than the detailed descriptions to be found in original sources.

Knauer (39), in a small volume which is decidedly less satisfactory in its illustrative materials, less convincing in its descriptions, and more popular than Brehm, has given a brief, readable account of the history of our knowledge of the apes, of their distribution, habits, and mental traits. An unusual feature of this work is its description of several widely known performing apes.

An article by Mahoudeau (53), chiefly historical, presents evidence for the conclusion that the African ape called gorilla by Hanno, the Carthaginian, was really a species of chimpanzee.

Aside from taxonomic works, which only incidentally and incompletely describe anthropoid behavior, no notable general contributions to this subject have appeared in English during the period of

this digest. Elliot's "Review of the Primates" (28) is an informational mine, but neither its psycho-biological descriptive materials nor its references suffice to carry the student far toward knowledge of behavior. The lack of a complete and reliable historical account of anthropoid behavior is an increasingly serious inconvenience to biologists. We therefore have assembled the materials and undertaken the composition of such a work. Somewhat to our surprise, hundreds of relatively inaccessible but more or less valuable sources contributory to knowledge of the natural history and psychobiology of the apes have been discovered.

CONTRIBUTIONS TO ANTHROPOID NATURAL HISTORY

Travelers, hunters, and naturalists continue to provide fragments of information on the manner of life of the apes. In the period of review there has been no single major contribution, although there are several which are distinctly worthy of note as containing some new observations or verification of previously recorded facts. Then, too, the apes have found their way into somewhat polite literature (Kearton, 37) and it is becoming increasingly difficult to distinguish between natural history and story.

What promised to be an exceptionally valuable contribution to the natural history of captive anthropoids and other primates was presaged by Pfungst (57) when in 1912 at the Berlin Congress for Experimental Psychology he presented a summary account of his studies of the behavior of some two hundred species of Old and New World primates in various German zoölogical gardens. So far as we have been able to discover, full report of his work has not been published.

Although Garner, long a prominent field observer of the African anthropoids, published several minor and popular articles between 1912 and his death in 1920, except for an account of the habits of the gorilla (30), they offer only materials previously published in his books. In connection with his hobby, the study of speech in infrahuman primates, Garner over half a lifetime intelligently and perseveringly studied the habits and life-history of the chimpanzee and gorilla. Because of his lack of scientific training and background and some serious inaccuracies of description, his books have been unfavorably criticised by biologists and their value has probably been underestimated.

There are few special contributions to the social relations of the manlike apes. Descamps (26) has offered a general discussion and Reichenow (59, 60, 61) has contributed valuably to the social psychology of the gorilla. From his experience as collector, Aschemeier (6) contrasts the behavior of the African great apes when attacked by man.

Among books which might be classified under travel, natural history, or story, because they partake of the qualities of each and are rapidly spreading knowledge of certain of the apes, are those of Akeley (1, 2, 3), Barns (8, 9), Bradley (15), Kearton (37), and Prince Wilhelm of Sweden (77). It is impossible to review these books adequately in this digest, but in later sections special mention will be made of their peculiar values as contributions to our knowledge.

Nests and nest construction in the apes have attracted a disproportionate amount of attention, but as a satisfying result information is now reasonably detailed and trustworthy. Certain, if not all, species and varieties of the three manlike apes build nests: the orang-utan and chimpanzee in trees, the gorilla sometimes in trees and sometimes on the ground.

The gibbon hides among leafy branches as do the monkeys. It is well established also that the orang-utan is primarily a tree-dweller, the gorilla primarily terrestrial, and the chimpanzee intermediate. From these types of ape the gibbon differs so extremely that it richly deserves separate consideration. Like the orang-utan, it is arboreal, but it is far more nimble and graceful in its movements.

Jennison (36), Burrell (19), and Yerkes and Learned (81) describe nest-building activities in captive chimpanzees, while Christy (23) briefly and critically comments on the work of Jennison. Reichenow (59), Aschemeier (7), and Barns (8) offer valuable contributions to our information about nesting habits in both the chimpanzee and gorilla. By Sokolowsky (70) the facts about anthropoid nest construction are systematically and comparatively considered. Although somewhat prolix his paper is the best single source of information.

The nature of most publications on anthropoid behavior suggests as basis of classification the type of animal studied. We shall therefore indicate, in brief paragraphs, the principal naturalistic contributions to our knowledge of the four types of ape.

Gibbon. Although he was interested chiefly in experimental study of vocalization and speech, Boutan (13, 14), in a gibbon which he kept for several years, was able to observe various forms of adaptive behavior. Unfortunately his reports give scant information aside from his experimental findings. A paper by Mahoudeau (51), although it contains no original observations, is useful as a summary, critical evaluation, and discussion of the work of others. It is mentioned here chiefly because the literature on the natural history of the gibbon is extremely meager. Shelford (67a) and Debeaupuis (25) offer interesting descriptions with certain fragments of new material, and in an unpublished manuscript, "The tree-walkers of the tropics," Mrs. Edith Taussig Spaeth reports the field and laboratory observations of Dr. Reynold A. Spaeth, whose promising program of work with the gibbons of Siam was cut short by his tragic death.

Orang-utan. Strangely few are the recent naturalistic studies of the orang-utan. There is a valuable paper by Kerbert (38) which deals chiefly with habits and life-history, and Shelford (67a) briefly considers general mode of life. Wallace's "Malay Archipelago" (76), the first edition of which appeared in 1869, we feel justified in mentioning here because the seventeenth edition or reprint appeared in 1922, but still more because during nearly sixty years it has stood as the best naturalistic description of the orang-utan.

Chimpanzee. In the period of this digest most naturalistic studies of the chimpanzee have been incidental to experimental inquiries and have therefore been carried on with captive animals. The following publications refine, if they do not greatly extend, our information about the habitat and the behavior of this, the most intimately known of the apes.

Comparisons of the chimpanzee with the gorilla, with respect chiefly to temperament, emotional expressions, and nesting habits, are offered by Aschemeier (6, 7) on the basis of his own observations. The animal trainer and showman, Sheak (65, 66, 67), contributes from his experience with the chimpanzee to our information about individual differences and docility in the most dramatic of the anthropoids. Noteworthy also are the

studies of life-history in the chimpanzee made by Montané (54) and von Allesch (4, 5).

Kohts (48, 49), Köhler (40–47) and Yerkes (80, 81), in connection with experimental studies of the chimpanzee, have had unique opportunity to observe daily life, individuality, disposition, and life-history. In their various publications they have presented materials which importantly supplement naturalistic descriptions.

It is not difficult to understand why during recent years the chimpanzee among anthropoid apes has monopolized the attention of experimentalists and the gorilla that of naturalists. The chimpanzee is relatively available, hardy, and coöperative in experimental work; the gorilla, by contrast, is relatively difficult to obtain, hard to accustom to confinement and to experiment with. Naturalistically speaking, the chimpanzee is well known, whereas the gorilla is imperfectly known and little understood.

Gorilla. The strictly naturalistic contributions to gorilla lore are both numerous and important. One of Garner's last reported professional undertakings was the capture of two young gorillas for the New York Zoölogical Park, one of which he finally succeeded in delivering to that institution in good condition. The event is notable because it was the result of a carefully thought out plan to capture specimens in Africa and there partially to domesticate them, accustom them to eat a variety of strange foods, and in general to prepare them for life in an American zoölogical park. Garner's experiences in taming and training the little gorillas, and his observations on diet, temperament, play and emotional expressions, have been simply and briefly recorded (30). A continuation of the story of the young gorilla brought by Garner to New York has been supplied by Hornaday (34), who, in addition to tracing the short history of the animal's life in America, contributes interesting general observations from his experience with other gorillas.

Reichenow (59, 60, 61) gives, by all odds, the most circumstantial and detailed description of the characteristics of the new-born gorilla and of the feeding and nesting habits of this ape. His observations bear more or less relation also to the development and condition of the senses and the appearance of various habits. In addition to rendering more certain our knowledge of gorilla nests and nest building, Aschemeier's papers (6, 7) report differences in temperament between the gorilla and chimpanzee and offer the opinion that the gorilla is not the less intelligent.

A healthy specimen of young gorilla during the World War came into the possession of Miss Alyse Cunningham of London, whose almost unique experience it was to keep the creature in good physical condition and contented until he became too large and difficult to manage in the household. Miss Cunningham's description (24) of John Daniel is of first-rate interest and practical importance. It is significant that this perfectly healthy young gorilla died within a few months after falling into the hands of the management of an American circus. The interest which Miss Cunningham's pet and her success with him stirred is evidenced in a measure by publications of Sir Ray Lankester (50) and Hornaday (35). Although she has published no additional reports, the writers happen to know that since the death of John Daniel she has kept for varying periods two other specimens of West Coast gorilla. Of these the first died from a head injury received in capture, and

the second, at last accounts, was in good health after some three years of life in captivity.

Reminding the reader of the days and exploits of Du Chaillu are the books of the collector-naturalist Barns (8, 9) whose knowledge of the mountain gorilla of the Belgian Congo is exceptional. His books contain the best available descriptions of the daily life of this rare anthropoid and of the history of our knowledge of it. Yet in this case even the "best" is extremely meager and unsatisfactory.

Almost simultaneously with the publications of Barns appeared accounts by Prince Wilhelm of Sweden (77) and Count Gyldenstolpe (31) of their expedition into the Lake Kivu region of the Belgian Congo in pursuit of gorillas. Hunting and killing is so conspicuous in their narratives that even though the information about the gorilla may be trustworthy, it is not likely to command the approval and confidence of the humane naturalist and conservationist.

Subsequent to the departure of the Prince of Sweden, but while Barns was still in the gorilla mountains, Akeley, representing the American Museum of Natural History in New York, conducted a small party thither with intent to secure a few specimens of the mountain gorilla for a habitat group in his Museum. The expedition has been delightfully described by one of its members, Mrs. Mary Hastings Bradley (15), who reports experiences in hunting gorillas. Akeley, in addition to several articles whose materials are largely second-hand, has published in his book "In Brightest Africa" (3) original observations and experiences in hunting *Gorilla beringei*.

Finally, the experiences of Benjamin Burbridge, hunter and nature lover, who has spent weeks in the country of the mountain gorilla hunting, observing, photographing, and capturing live specimens, have been partially recorded by him (18a) and by Sparks (73). From conversation with Mr. Burbridge we have discovered that he knows a great deal about the characteristics and life habits of the mountain gorilla which thus far he has neglected to record. He is distinguished also by having secured excellent motion pictures of mountain gorillas in the wild, and not less so by having taken alive eight specimens of the young of the species!

LIFE-HISTORY AND GENETIC RELATIONS

Few indeed are the significant contributions to the life-history and genetic relations of the anthropoid apes. In the period of digest the first paper to be noted is that of Montané (54, 55) who from the Abreu primate colony in Havana obtained data on the sex behavior and breeding of chimpanzees. He was the first to report the birth and early behavior of Anumá, the only chimpanzee known to have been born and reared in the Western Hemisphere. Most of the data presented by Montané still lack confirmation.

Blair (12) from the New York Zoölogical Park, and von Allesch (4, 5) from the Berlin Zoölogical Garden, report on chimpanzee pregnancies and the birth of young. In New York the young survived birth for only a short time, whereas in Berlin von Allesch had opportunity to study the behavior of mother and young over a period of weeks. In his general account of the Abreu primate colony and of our knowledge of affective behavior in the anthropoid apes, Yerkes (80) has devoted to the life-history of the anthropoids a chapter in which are assembled available facts concerning the period of gestation, infancy, and parental relations.

From these several contributions it

appears that the period of gestation in the chimpanzee is not less than seven, nor more than nine, months, that the newborn animal is practically helpless, and without parental attention and assistance perishes within a few hours. During the first few months of postnatal existence it is wholly dependent on the mother for nourishment, protection, and bodily care. Gradually it achieves independence through acquisition of ability to walk, in which it is assisted by parental tuition and is thus enabled to amuse itself in increasing measure, to seek food, and to develop steadily through play with others of its kind.

Publications of Reichenow (61) and Garner (30) are contributory rather to our knowledge of behavior in the young of the gorilla than to generation or parental relations.

STRENGTH, ENDURANCE, HEALTH

There is widespread conviction that the great apes are very strong, but until recently no measurements had been reported. In two papers by Bauman (10, 11) dynamometric measurements of the strength of the chimpanzee and orang-utan in comparison with that of man are offered. The procedure was far from satisfactory and the data are indicative merely of the order of strength. Whereas the maximum pull for an adult female chimpanzee was 1260 pounds, both arms being used, that for the average college man is 332 pounds. The author states that the chimpanzee's superiority to man on the basis of weight is in the ratio of three to one.

Unpublished observations by Yerkes indicate that the young mountain gorilla is, relative to weight, much stronger than man. These observations on strength suggest the important physiological question: By virtue of what circumstances of life or structural peculiarities are the muscular or the neuro-muscular mechanisms of the orang-utan, chimpanzee, and gorilla so far superior in working power to those of man, or is the seeming superiority to be accounted for by relative use?

Evidences of fatigue in the apes, especially in experimental situations which require novel adaptations of behavior, have been noted by various observers but never described with useful detail and exactitude. Boutan (13, 14) states that mental work rapidly fatigues the gibbon and induces yawning and finally sleep, and Yerkes has made similar observations on the chimpanzee and other primates.

Anthropoid diseases, health, and hygiene have not been systematically and adequately discussed by any single authority. The special chapters devoted by Yerkes (80) to this subject are perhaps as useful practically as anything available. He has dealt especially with environmental requirements of captive apes, covering nutritional, hygienic, and social factors. There are, to be sure, many references to diseases characteristic of the apes, and papers descriptive of pathogenic organisms which are commonly or rarely discovered in them. We have considered it inappropriate to include literature on parasitology or medicine in this digest.

From the various reports available to us and certain unpublished observations, we gather that the anthropoid apes in general are susceptible to many of the diseases of man and suffer peculiarly from them because of lack of protective immunity and ordinarily good physical condition and care. Mortality, we suspect, may be due more largely to the unfavorable conditions of captivity than to greater susceptibility to disease or even to lack of immunity. Our scanty knowledge

points to the conclusion that captive apes demand intelligent, scientifically based nutritional, hygienic, and social provisions, including shelter from the direct sun and from unusual cold or wet. There is nothing to prove that they are less adaptable than man or less capable of normal life and reproduction under varied climatic and social conditions.

PSYCHO-BIOLOGY OF SENSORY AND PERCEPTUAL PHENOMENA

Apart from naturalistic observations of sensory equipment and perceptual activity, there are few contributions to the psychophysiology of the senses in apes. Many authors intimate that their special senses are similar to those of man, but the evidence is scientifically inadequate. Indeed even the best of the experimental inquiries are technically weak and must be considered exploratory rather than conclusive.

The existence of highly developed senses of sight, hearing, taste, touch, and smell is amply attested by numerous naturalistic observers, among whom mention may be made of Barns (8, 9), Descamps (26), Debeaupuis (25), and Kearton (37). Furness (29) claims to have demonstrated color discrimination in the chimpanzee and orang-utan, using painted blocks. With the aid of a form-board he studied also visual discrimination of form. Attempts to teach his subjects to reproduce simple drawings and to tie knots, demanding unusual visual-motor connections, yielded few positive results.

The most extensive study of the psychobiology of vision in an ape is that of Kohts (48, 49). This investigator experimented with a young chimpanzee in an attempt to measure his ability to detect and react appropriately to color, brightness, form, size, and number. Complete account has thus far been published only of her study of color and brightness discrimination. The work was carried on in Moscow during the World War and it was impossible for Mrs. Kohts to command adequate technical resources. She therefore made use of the best available colored and neutral papers and painted objects.

The method employed by Kohts is novel, although not wholly new, and her use of it establishes its value for exploratory and qualitative work, if not for rigidly controlled and precise measurement. She calls it the method of "choice from sample." The animal was trained to sit at a table opposite the experimenter. On the table was placed an assemblage of objects to which the animal was taught to react by selecting and manually presenting to the experimenter one which in a given quality matched an object previously displayed by the experimenter as sample. Clearly the presentation of the sample object is equivalent to a command to match it from the objects available on the table. It is necessary then for the animal to search visually or otherwise for the appropriate object and on recognition to hand it to the experimenter.

Kohts, keenly aware of several possible sources of error, effectively checked her results in various ways. The visual stimuli which she necessarily depended upon are not readily describable with scientific accuracy, nor can they be duplicated easily by other investigators. There is also a possibility that the chimpanzee may have obtained certain assistance in the form of sensory cues unconsciously given by the experimenter.

The observations of Kohts, as summarized in her voluminous report, prove the ability of the chimpanzee to react specifically to wave-length (color or hue) versus intensity (brightness). Also that chromatic stimuli, closely similar in hue but differing markedly in satura-

tion, are more readily distinguished than are those which differ markedly in brightness but are very similar in saturation. The investigator believes she has demonstrated that the chimpanzee naturally depends rather on hue than on brightness in its response to colored objects. The degree of acuity in wave-length (color) versus intensity discrimination it was impossible to measure satisfactorily because of the nature of the experimental materials.

Worthy of note because of its unexpectedness is Kohts' conclusion that achromatic visual stimuli, with the possible exception of white and black, are not as readily distinguished by the chimpanzee as are chromatic stimuli.

Her investigation demonstrates with reasonable certainty the existence of color sense in the chimpanzee, but it fails to provide such detailed and reasonably accurate measurements of the value of different aspects or factors in visual stimulation as are desirable and essential for comparison of the visual equipment of the chimpanzee with that of man and other animals.

The experiments on visual discrimination of form, size, and number carried on by Kohts with the chimpanzee Ioni are only summarily described in her available publications. We are informed detailed report is in course of publication. With respect to these aspects of vision the investigator states that by the method of choice from sample she was able in a surprisingly short time to make a very large number of experiments which, in addition to the results above referred to, demonstrated ability to recognize and discriminate various planimetric and stereometric figures, objects differing in volume or in one of their three dimensions, and such objects as letters and pictures.

In brief, Kohts believes that she has proved that the visual equipment of the chimpanzee is, in its essentials, similar to that of man. As measurements of acuity were not made, it is impossible to go beyond this qualitative statement.

The experimental investigation of Kohts is the first detailed, systematic, reasonably thorough-going and highly illuminating investigation of the sensory life of an anthropoid ape. Whatever its technical shortcomings may be, its results are valuable as indication of the outstanding characteristics of chimpanzee vision and as basis for the formulation of specific problems in the study of this sense.

At the Canary Island Anthropoid Station Köhler (40, 42), working with chimpanzees, concentrated his attention on problems of perception, memory, and imagination, and more or less incidentally discovered sensory characteristics. Taking his cues from the characteristics of human vision and his problems from the classical literature of the psycho-physiology of visual perception, Köhler planned and carried out certain extraordinarily illuminating investigations. His work was done in the main under unusually trying conditions.

Response to achromatic stimuli, supplied by a standard series of neutral papers ranging from intense white to dead black, demonstrated, in agreement with the observations of Kohts, the ability of the chimpanzee to discriminate on the basis of small differences in brightness. Experimental procedure, although crude perforce of circumstances, was ingeniously checked and there can be little doubt of the reliability of the findings, although as in the case of those of Kohts, the statements of result are primarily qualitative.

Köhler presented, as stimulus objects, two adjacent boxes, the visual appear-

ance of which could be readily altered. The animal, by reaching for the desired box with a stick and drawing it to the netting through which the hand could be reached, secured as reward for correct choice a bit of some desired food. The box designated as the wrong one contained no food. Punishment for incorrect choices was not employed and the investigator doubts its efficacy with the chimpanzee.

Somewhat similarly, Köhler investigated the chimpanzee's ability to discriminate chromatic stimuli and to his satisfaction demonstrated, through positive results with red, blue, and mixtures thereof, the existence of color sense. In this case the materials were painted surfaces prepared at the station by Köhler and impossible of exact description with his facilities. The stimuli were presented behind circular openings ten centimeters in diameter in two like adjacent boxes. Color wheels, rotated to give complete fusion for human observers, were employed to produce the stimuli intermediate between the terminal blue and the terminal red. On its part, the animal was required to point either with arm or stick to the box which it selected as correct. Thereupon a food container was delivered to it by the experimenter. In case of correct choice this container supplied a reward; otherwise it was empty.

By comparison with his other contributions to the psychobiology of the chimpanzee, Köhler's studies of color and brightness vision are of minor importance. Yet because of the meagerness of our information the work commands critical and appreciative consideration.

With Kohts, Köhler agrees in concluding that discrimination on the basis of color is easier to the chimpanzee than similar discrimination on the basis of achromatic stimuli.

Only incidentally do the visual investigations of Kohts and Köhler contribute to our knowledge of the other senses in the chimpanzee. Hearing is relied on constantly as a guiding sense, but there is no convincing evidence that the animals use smell to supplement visual discrimination and choice. Both smell and taste, however, are regularly employed in testing objects which the animal suspects of being edible.

In the realm of visual perception the contributions of Köhler are epoch-making and undoubtedly will have a profound influence on the development of comparative psychology. Working with extremely meager instrumental equipment and resources, he displayed ingenuity and skill which should stimulate and inspire those who labor in poorly equipped laboratories.

Monocular vision was tested by placing the reward, a banana, at variable distances behind a wire screen before which the animal stood. To the animal in this position the experimenter handed two sticks, the one capable of being fitted into the other, so that the united pieces might be used to fish through the screen for the food. The subject was required to fit the pieces together: (1) with binocular vision; (2) with monocular vision; and the time required for the process was recorded as a measure of the value of visual function. The chimpanzee Sultan, a right-handed animal, yielded the following results: Time for binocular vision, 2.1 seconds; for monocular vision, right eye, 3.4 seconds; for monocular vision, left eye, 5 seconds.

In tests of visual perception of depth, it was demonstrated by an ideally simple procedure that a desired object could be correctly located in 84 per cent of choices with binocular vision; in 53.3 per cent with monocular vision, and in the case of a right-handed chimpanzee 58.3 per cent

with the right eye alone, and 48.7 per cent with the left eye alone.

In this experiment the chimpanzee was allowed to stand before a screen in which a small hole at the level of the eye permitted it to see a grape which was suspended on an invisible thread in the midst of a chamber. It was necessary for the animal visually to locate the grape as dropping either before or behind a screen which divided the stimulus chamber into two compartments. The subject in seeking its reward went, according to its perceptual data, either to the nearer or the farther division.

The question: Can an object be recognized by a chimpanzee as the larger of two familiar objects, even though its corresponding retinal image be the smaller? was affirmatively answered by the following experimental procedure.

On a table behind a wire screen, before which the animal worked, were placed two stimulus boards which constituted the visible fronts of food containers. The one board was much larger than the other. In the first instance the animal was trained to choose the larger box in order to get reward of food. Thereupon, the boxes were shifted in position so that the smaller was relatively nearer the screen and its image larger than that of the objectively larger board. Assuming that the animal is discriminating on the basis of visual size, this reversal in the relative size of the images of right and wrong boards should be followed by consistent choice of the objectively smaller stimulus area. The chimpanzee, however, continued to choose the larger board in spite of all changes in position, reacting thus as does man, and demonstrating presumably the existence of cortical or memory factors or contributions which either replace or supplement the immediately presented visual stimulus and constitute adequate basis for correct reaction.

Maintenance of the identity of visual objects amidst diversity of conditions Köhler demonstrated also in an experiment on the discrimination of widely differing neutral or achromatic stimuli. In this instance the one food container presented a white front to the animal and the other a black front. The animal was trained to choose the white as the correct reward-containing box. When this habit had been established, the experimenter suddenly altered the relative luminosity of the two stimulus surfaces by permitting direct sunlight to fall on the black surface. Thus it became relatively white and the other relatively black. The chimpanzee, nevertheless, continued to choose correctly, demonstrating the existence of other than the primary visual factor in its discrimination, and definitely raising the question of memory contribution.

Köhler's investigations occupied years and it is impossible within the limits of this digest to do more than characterize his methods and results in the study of sensation and perception and to exhibit them by samples. Even more significant in essential respects than his notable contributions of fact are his critical discussions of the historical methods of investigating sensory discrimination and acuity in infrahuman organisms and his suggestion of other experimental procedures.

STUDIES OF ADAPTIVE BEHAVIOR

Adaptive behavior, as here used, includes all conditioning of action from the modification of simple reflexes to the development of complex habit-systems which may involve ideation and purpose. The lay term 'intelligence' is generally applicable, but it is scarcely inclusive enough and its degree of applicability varies widely.

Observations relative to adaptive behavior in the anthropoid apes appear in a large proportion of the naturalistic

publications, and the writings of animal trainers are dominated by facts and reflections concerning the exceptional intelligence of the chimpanzee or other anthropoid. Peculiar, however, to the period of this digest is the appearance of several major experimental contributions to the subject. Without intending to disparage naturalistic work, or indeed the utilization of any opportunity to gain knowledge of anthropoid behavior, one may reasonably contend that definitely directed and controlled systematic and sustained study of various kinds or aspects of adaptive behavior in the apes is of preëminent importance and should rapidly refine, extend, and illuminate our knowledge.

To begin with certain relatively minor contributions—Haggerty (32), taking his cues from Hobhouse (33), by simple experimental procedure tested, in the New York Zoölogical Park, the ability of a chimpanzee and orang-utan to use a stick as a tool. Also he noted evidences of adaptive behavior in the daily life of his subjects. By his results, which were incidental to systematic experimental study of the imitative tendency in monkeys, he was led to believe that the orang-utan is superior in intelligence to the chimpanzee and that the behavior of both suggests perception of relations, a low order of rationality, and ability to profit by experience by something more closely akin to understanding of the situation than to the blind efforts of trial-and-error.

Acquaintance with the orang-utan having suggested to him its capability of indefinite profiting by educative treatment, Furness (29) undertook to acquaint himself intimately with examples of both the orang-utan and chimpanzee, and to train them by kindergarten methods to speak, read, and write. His experimental technique, although apparently adequate to his purpose, yielded little but negative results. In the course of the work he demonstrated various types of adaptation and became impressed with the ability of the animals to regulate their actions in accordance with sensory discriminations and perceptions essentially like our own.

In the end Furness concluded that his apes showed no "signs of reasoning." Yet in the same paragraph he states: "I am inclined to think, however, that such an act (unlocking door, turning spigot, etc., to get a drink of water) with the chimpanzee is governed by simple succession of ideas rather than by a prearranged sequence of actions, with a definite object in view." This statement enables one to evaluate the author's contribution to psychobiology.

Working also with orang-utans and chimpanzees, Shepherd (68, 69) in his application of simple experimental tests which he had previously used on monkeys, dogs, and cats, obtained results indicative of ideas, "probably of a crude and unanalyzed type." Shepherd and also Sheak (65, 66, 67), from observation of animals trained for the stage, have made observations pertinent to adaptive behavior. On this score Sheak's intimate acquaintance with performing animals entitles his statements of fact and his conclusions to serious consideration.

The first and only experimental study of adaptive behavior in the gibbon is that of Boutan (13, 14) who for five years carefully observed the daily life and adaptations of a female of the species, *H. leucogenys*. His initial interest was in vocalization, but he was presently led to undertake a comparative and experimental study of adaptive behavior in the gibbon and young child.

The methods of Boutan in this pioneer comparative work evidently were sug-

gested by the investigations of Thorndike and Kinnaman. They involved the use of problem boxes, each of which presented a relatively simple mechanism, by the proper manipulation of which food might be obtained from within the box. In some cases the mechanism was visible to the subject; in others, invisible. Boutan's observations bear the marks of critical care and his conclusions are of such considerable theoretical importance and have been so far ignored or neglected by psychobiologists that they are presented herewith in free abbreviated translation.

Boutan's principal conclusions (14, p. 142–43). (1) In these experiments the gibbon acquired by its own initiative new ideas. (2) It remembered the new ideas and the movements appropriate to the activity which led to their discovery. (3) The animal had prevision of the object to be attained, but not of the movements necessary. In its consciousness the idea of movement appears to be independent of the movement itself. (4) Under ordinary circumstances the animal manifests spontaneous or natural attention. (5) In exceptional cases one observes the beginnings of voluntary or artificial attention. (6) These flashes of the characteristically human sort of attention cause the animal great physical fatigue. (7) The young child *who has not learned to speak* works like the gibbon. Its performance seems even inferior to that of the ape; it opened the box with invisible mechanism as did the gibbon in the first period of work. (8) The child *who is beginning to talk* does not work like the ape. Instead its efforts are directed along a definite line. Its performance with the invisible mechanism is inferior to that of the ape and of the younger child. (9) The child who is beginning to speak works like a man; the child who does not speak works like an anthropoid. (10) The difference in method appears to be due not to difference in age but to conditions associated with the possession or lack of language.

With the definite intention of studying in contrast the method of solution of standardized problems by monkey and ape, Yerkes (78) for a number of months experimented with a young orang-utan. He used an original method known in the literature as the multiple-choice method, and supplemented his results by employing also a variety of simple problem tests, such as are commonly used by lay observers, by animal trainers or by psychologists whose curiosity impels them to do something with anthropoid apes.

By the multiple-choice method the investigator is enabled to present to any type or condition of vertebrate whose adaptive behavior he may wish to study, one or all of a series of problems ranging from simple to complex. All the problems are perfectly and quickly soluble by an organism which is capable of perceiving certain essential relations and of acting as does man when he experiences insight or the understanding of a significant relationship.

In this carefully planned type of experimental situation the behavior of the young orang-utan in some respects closely resembled that of man. Yerkes has cited the following as evidences of ideation: (1) Trial by the animal of several different methods in connection with each problem; (2) sudden transition from one method to another; (3) the final and perfect solution of a problem without diminution of initial errors; (4) the dissociation of the act of turning in a circle from that of standing in front of a particular box. Further, this investigator states: "The survey of my experimental records and supplementary notes forces me to conclude that as contrasted with the monkeys and

other mammals, the orang-utan is capable of expressing free ideas in considerable number, and of using them in ways highly indicative of thought processes, possibly even of the rational order. But contrasted with that of man, the ideational life of the orang-utan seems poverty-stricken. Certainly in this respect Julius [an orang-utan] was not above the level of the normal three-year-old child" (78, p. 132).

Although in her intensive study of the young chimpanzee Kohts was concerned chiefly with characteristics of vision, she incidentally observed many and varied evidences of adaptation of behavior, and in a few cases especially modified her experimental procedure to exhibit whatever types of adaptation the subject might be capable of. Thus, for example, instead of leaving the sample object which was to be matched by the animal in sight during the matching activity, she would display it for a few seconds, remove it from view, and delay the chimpanzee's reaction for a definite period in order to measure his ability to respond correctly under such conditions. It was found that correct choice continued up to approximately fifteen seconds delay, but beyond twenty seconds the ape usually responded incorrectly.

Experiments of Kohts, in which the ape was required to select the correct object by some one quality, as for example color, from among a group of objects differing in form, size, and color, indicate, she believes, certain limited power of abstraction. The presence of ideas is inferred from the characteristics of the animal's adaptive behavior, and it is stated that the practical conclusions arrived at by the animal seem to be based on something akin to thought processes.

In general the evidences of ideational behavior in this anthropoid reported by Kohts, and her conclusions, are similar to those of the more thoughtful and critical of naturalistic observers, animal trainers, and psychologists who have applied certain simple tests of intelligence.

Köhler, during his prolonged period of service at the Canary Island Anthropoid Station, devoted a large portion of his time to experimental analysis of adaptive behavior in the chimpanzee. Fortunately, he had several healthy immature animals and was able to compare individual differences and, in a measure at least, to escape the undesirable human influence which to an indefinite extent vitiates work with animals trained for the stage. Throughout his prolonged investigation he apparently kept in mind the question: Does the chimpanzee act with insight under conditions which require it?

In securing evidence of the ability of his animals to solve novel problems and in gaining accurate knowledge of their methods of solution, Köhler used not only the types of simple test procedure previously suggested or used by Romanes, Hobhouse (33), and others, but added many ingenious and appropriate situations of his own invention. He did not, however, despite abundant and excellent opportunity, use the method of insoluble problems devised by Hamilton (Jour. An. Beh., **1**, 33), the delayed reaction method of Hunter (Beh. Monos., serial no. 6), or the multiple-choice method of Yerkes (Jour. An. Beh., **7**, 11).

According to Köhler's classification (41), he depended upon four principal types of problem method, designated by him as round-about methods, the use of implements, the making of implements, and detours around separate intervening objects. In each case, the essential feature of the situation is the possibility of securing reward by the performance of an act which depends upon the perception of

some important relationship. For example, a banana, lying outside the cage and beyond arm's reach, may be obtained by using a stick which lies on the floor of the cage; or, in another experiment, by straightening a bent wire and using it to reach and pull with. Or, a food container may be brought within reach by going to a remote corner of the cage and unhooking a rope which supports the container. Food suspended from the ceiling of the cage may be reached by the stacking of available boxes or by the use of a ladder. Obstructions in some instances may have to be removed or so placed that they will serve a useful purpose.

The author's detailed descriptions of the behavior of his animals in the numerous and extremely varied problem-situations are illuminating beyond comparison with any previous work, and his results and conclusions are entirely consonant with those of other authorities who have studied experimentally the chimpanzee and orang-utan (see 32, 49, 69, 78, 80).

As his principal conclusion from the study of adaptive behavior, Köhler states that the chimpanzee exhibits intelligent behavior which in man is accepted as indicative of insight, understanding, and the functioning of ideas. He takes pains to point out that his observations are consistent with the prevalent conception of organic evolution and support the correlation of intelligence with brain structure. The lack of speech is singled out as one of the chimpanzee's chief disadvantages by comparison with man, and next to it the absence of our sort of visual space forms with appropriate relations to motor processes makes the human world a very confusing place for the ape.

This brief objective description of Köhler's contribution to anthropoid psycho-biology seems hopelessly inadequate. His work is in a sense epoch-making, because it displays ingenuity, adaptiveness, insight, constructive imagination, power of self-criticism as well as of the methods and conclusions of others.

The first experimental study of the gorilla, involving measurement of adaptivity and systematic observation of habits in captivity and of emotional expressions, was begun by Yerkes near the close of the period of this digest. The results, now in press,[1] although limited to a single specimen of the mountain gorilla, will afford a better basis for comparison of this rare ape with other types of primate than did previous naturalistic observation.

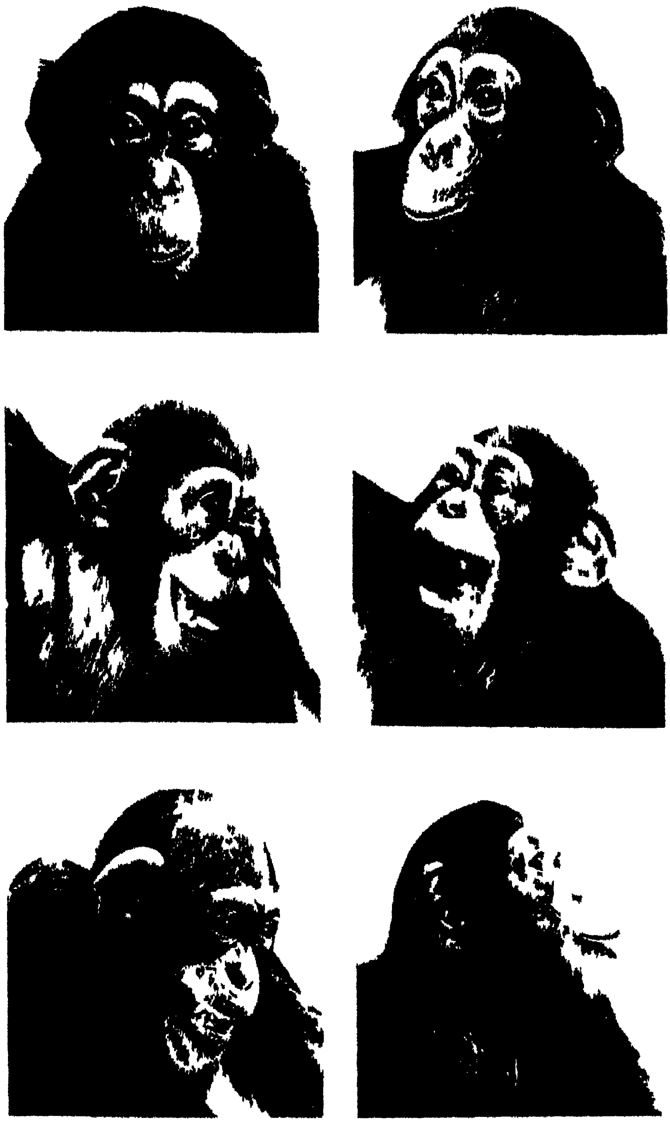
Yerkes and Learned (81), in a report which is chiefly devoted to vocal expressions and their significance in the chimpanzee, present evidences of adaptive behavior gained from observation of the daily life of their animals and from experimental studies directed to the exhibition of adaptivity and the demonstration of whatever ability the animals may have to work from insight.

TEMPERAMENT, DISPOSITION, AND EMOTIONAL EXPRESSIONS

Many of the naturalistic papers descriptive of the habits and environmental relations of the apes contribute fragmentarily to our knowledge of disposition and emotional expressions. The following references are worthy of mention: Aschemeier (6), Barns (8, 9), Boutan (13), Cunningham (24), Garner (30), Hornaday (35), Kearton (37), Lankester (50), Reichenow (61), Rothmann and Teuber (64), Sokolowsky (70), and Sparks (73).

In a description of the disposition of

[1] Genetic Psychology Monographs.



Courtesy of Mrs. Kohts

EMOTIONAL EXPRESSIONS OF IONI, A FIVE-YEAR-OLD CHIMPANZEE OBSERVED BY MRS LADYGIN-KOHTS IN MOSCOW

chimpanzees Sheak (65) considers individuality and temperamental traits in captive specimens which he has known.

For the young orang-utan Yerkes (78) records temperamental characteristics and emotional expressions under ordinary conditions of life in captivity and in experimental situations as well. The affective characteristics of two young chimpanzees are described by Yerkes and Learned (81), and in a somewhat more general and systematic work Yerkes (80) gives an account of the emotional life of the chimpanzee and orang-utan, based on observations at the Abreu primate colony and on the data of the available literature.

Kohts (49) and Köhler (41, 44), working simultaneously with chimpanzees, have contributed important facts of affectivity. Their careful descriptions make clear the conspicuousness of individual differences and the similarity of the apes to man in temperamental constitution and in dominant emotional expressions. Kohts states as her opinion that the chimpanzee more closely resembles man in its affective than in its intellectual life. She obtained in connection with her experiments and has published (49) some splendid photographs of emotional expression in the chimpanzee.

VOCALIZATION, SPEECH, LANGUAGE

Garner, the outstanding specialist on speech in infrahuman primates, published nothing on this subject within the period of our digest. His notable books, which, like the famous DuChaillu description of the gorilla, have been unfavorably and perhaps also unfairly criticised by the scientific world, antedate this period. No one has seen fit to follow in Garner's footsteps by making the study of primate speech a hobby. The subject, however, has not been wholly neglected and there are several publications which deserve comment.

Following general observation of the vocalizations of the chimpanzee and orang-utan, Furness (29) attempted by various means to teach specimens of these apes to talk. By diligent effort he succeeded in getting them to pronounce two or three words. Although discouraged by their slow response to training, this observer concludes (1) that the orang-utan is more promising as a conversationalist than the chimpanzee because it is the more patient, less excitable, and takes more kindly to instruction; and (2) that in comprehension of the significance of words for objects and actions, the orang-utan and chimpanzee exceed domesticated animals. He states that both of his apes were able to understand what was said to them better than any professionally trained animals he had ever seen.

The vocalizations of the gibbon, often commented on by travelers because of their unusual quality, have been well described by Mahoudeau (52). With special interest in the origin of language and of the relation of vocalization in the other primates to speech in man, Boutan (13) for some years studied the vocal expressions of the gibbon. The title of his report "Pseudo-language" suggests his principal conclusion. He discovered that the animal is capable of varied vocalizations which may be classified as: (1) Expressions of satisfaction and well-being; (2) expressions of discomfort, illness, or fear; (3) expressions indicative of intermediate conditions, and (4) expressions of great excitement. He states that the characteristic sounds made by the wild gibbon are innate and not the result of parental education or imitation of the behavior of its fellows. He further is convinced by his observations that this ape does not use sounds in a verbal sense,

as symbols of objects or actions, but merely as expressive of emotions. Boutan's monograph on pseudo-language is at once the most interesting and the most valuable of the studies of vocal expression in this type of ape.

The most recent published account of chimpanzee vocalizations and effort to teach this ape to speak is that of Yerkes and Learned (81). The latter recorded in musical notation the various vocalizations of two young chimpanzees, seeking also to discover the significance of the sounds; and the former undertook by simple experimental procedures to train one of the animals to reproduce sounds in association with objects. The results of this instructional attempt were almost wholly negative and they convinced the investigator of the slight tendency in this ape to reproduce auditory stimuli or to imitate sounds produced by its kind or by man. This record of chimpanzee vocalization is uniquely valuable because of its relative completeness and its definite information as to the quality and natural uses of the voice in the young of the chimpanzee.

In a general chapter on anthropoid speech and its significance, Yerkes (80, p. 165) offers a résumé of notable contributions, and attempts to indicate definitely the present status of our knowledge. His discussion concludes with the statement: "Everything seems to indicate that their vocalizations do not constitute true language, in the sense in which Boutan uses the term. Apparently the sounds are primarily innate emotional expressions. This is surprising in view of the evidence that they have ideas, and may on occasion act with insight. We may not safely assume that they have nothing but feelings to express, or even that their word-like sounds always lack ideational meaning. Perhaps the chief reason for the ape's failure to develop speech is the absence of a tendency to imitate sounds. Seeing strongly stimulates to imitation; but hearing seems to have no such effect. I am inclined to conclude from the various evidences that the great apes have plenty to talk about, but no gift for the use of sounds to represent individual, as contrasted with racial, feelings or ideas. Perhaps they can be taught to use their fingers, somewhat as does the deaf and dumb person, and thus helped to acquire a simple, nonvocal, 'sign language.' "

SOCIAL RELATIONS AND INSTITUTIONS

Only one article devoted exclusively to sociological considerations has been found. It is that of Descamps (26) who briefly compares social phenomena in the anthropoid apes with those in primitive man. The principal categories of social phenomena used by this author are: means of existence, mode of existence, and group life. In each, marked similarities as well as differences among the types of anthropoid ape and between them and primitive man are noted. Although this author makes no contribution to our knowledge of social relations in the apes, his discussion convinces one of the great importance and promise of this field of inquiry and stirs interest.

From his sustained observation of immature chimpanzees Köhler contributes significantly to anthropoid sociology. He was able to observe the social behavior of young animals, both male and female, but had no opportunity to study parental or family relations. This is equally true of Yerkes (81) who noted various relations between his two young chimpanzees, and also the attitude of each toward other creatures in their environment. The contribution of Kohts, since she worked with a single ape, is limited to its behavior and relations to other types of organism.

Drawing his materials largely from the

chimpanzee group in the Abreu anthropoid colony, Yerkes (80) has been able to describe somewhat more fully and systematically the relations between apes of the same or different age, between the sexes, in the family group, and between father and offspring and mother and offspring. This account, although far from complete and doubtless wholly inadequate in many other respects, advances the subject by bringing together scattered observations and by supplementing it in the light of the occurrences in an extraordinarily interesting anthropoid colony.

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STUDIES IN THE GENERAL PHYSIOLOGY AND GENETICS OF BUTTERFLIES

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INTRODUCTION

THE exquisite colors of diurnal butterflies are such a source of pleasure to the collector that the amateur is often content with the classification and description of his dried specimens. But to one who has watched day by day the growth and transformations of many butterflies, such a collection in spite of its beauty seems like a gorgeous mausoleum. One misses the reactions of the graceful live creatures in response to sunlight and shadow, to the varying lure of different flowers, to their mates, to man and other giants which invade their field of vision.

Each live butterfly has its personality. It behaves, in the first place, according to the customs of its own family, genus and species, for the instincts of each clan differ strikingly as we shall see. It differs, moreover, from other representatives of its own species and even its own brothers and sisters, in vigor, longevity, fondness of the other sex and of its food, its response to light and shade.

Let us take for example the colony of caterpillars of *Vanessa antiopa* from the same mother, which I brought into the laboratory in June, 1924. They emerged as adults within two or three days of each other during the first week in July. A few caterpillars had died of wilt or *flacherie*, a boon to the farmer but a pest to the silk raiser and student of genetics, to which one male butterfly succumbed a few days after eclosion.

LONGEVITY

This group of butterflies was under observation in the greenhouse for six months,—the last survivor living until Christmas—in a cage 18 inches square, consisting of a frame covered with soft netting. A bunch of fresh flowers dipped two or three times a day in water sweetened with brown sugar to the consistency of maple sap was always within their reach at the top of the cage. Deaths occurred as follows:

	sex	*age*
September 6..............	female	2 months
November 10..............	female	4 months
November 10..............	female	

Meanwhile out-of-doors fresh antiopas of the second or autumn generation had appeared. The little colony in the laboratory had outlived the usually recognized limits of its own generation. One was killed by accident; one escaped; the remainder lived until the following dates:

November 18.....	male	20 wks.	$= 4\frac{1}{2}$ mos.
November 20.....	female	20 wks.	
November 26.....	female	21 wks.	$= 4\frac{3}{4}$ mos.
December 6.....	female	22 wks.	$= 5$ mos.
December 19..	2 females	24 wks.	$= 5\frac{1}{2}$ mos.
December 22.....	female		

The last survivor was still alive, though feeble, on December 24, aged 25 weeks,

or about 6 months. This is probably not unusual in this species and a few allied species which hibernate as adults. The autumn brood regularly hibernates, and Dolley (1916) also records that six individuals of *Antiopa* lived in his laboratory from August to the latter part of February, that is, for six months.

The normal life of an adult butterfly of *Colias philodice*, however, is much shorter than of *Vanessa antiopa*, an average of not over three weeks in summer; it is prolonged somewhat by cold conditions. Hibernation, however, very rarely occurs at this stage, and I have never succeeded in wintering the pupa. The young larva in the second or third stage regularly hibernates.

Seven sisters eclosing the last of June (in 1921) lived from 15 to 28 days with an average of 18½; three others in April–May lived an average of 20 days, which may be regarded as about the normal period. Three sisters eclosing the last of August (in 1920) lived, however, an average of 27⅔ days, ranging from 23 to 33. The record for longevity of a female in activity was six weeks (August 23–October 5) during the autumn.

The most interesting features of the behavior of this colony of *V. antiopa* were their extraordinary stereotropism, or "death-feigning" instinct, their gregariousness, or tendency to gather in clusters like the caterpillars of this species, and their geotropic posture while at rest (corresponding to the head-downward position of the pupa).

STEREOTROPISM

When a butterfly of the genus *Colias* with its wings closed over its back is carefully laid upon its side upon a flat horizontal surface, it will lie quietly, provided it is not overexcited and its feet are not stimulated by contact with something solid. This instinct is far more highly developed in *V. antiopa* than in *Colias philodice* and *C. eurytheme*. When picked up by the wings and placed sidewise upon a table or upon a bunch of flowers, *Antiopa* draws in its feet and lies in a passive, inert state. If the light and heat are not intense, it may be tossed about without response, like any "death-feigning" insect, and will lie for a long time on its side. Gentle pressure upon the under side of the closed wings produces this quieting effect; even lifting the butterfly by the costal margins of the closed wings is sufficient to make it draw up its legs against the body and come to rest. I have found also that certain moths which spread their wings horizontally when at rest, if carefully inverted so that the upper surfaces of the wings are under gentle pressure, will lie quietly upside down, provided their feet are not stimulated by contact with any solid object.

This instinct in its incipient stages can hardly be regarded as protective and useful. It is the very simple quieting effect upon the neuro-muscular system produced by gentle pressure upon the wing surfaces, an inhibitory reflex, resulting in rest.

GREGARIOUSNESS AND POSTURE AT NIGHT

Gregariousness in *Vanessa antiopa* appears in their strong tendency to creep together into close clusters in the corners of the cage, usually toward the source of light. Compact groups of individuals resting head downward are regularly found in the cage at night. *Colias* never does this; they are always well scattered at night over the flowers in the cage and upon its walls, showing a strong tendency to hang wings downward, but not, as a rule, head downward. The wings-downward position is the characteristic nocturnal habit in *Colias* in the fields. Rest-

ing in this way, the wings are well protected even from torrents of rain. I have not investigated the reason for gregariousness, which is quite a different thing from the positive phototropism common to all butterflies in flying in bright sunlight and which brings *Colias* together at the top of a cage under such conditions. It is perhaps an olfactory attraction, and may be the same tropism which, in *Antiopa*, holds together in a colony the caterpillars from a single laying of eggs.

GEOTROPISM IN ANTIOPA

The third striking characteristic of *Antiopa* is the head-downward position when at rest. Parker (1903) has described this as negative phototropism, the head, after the butterfly has alighted, being turned away from the source of light. The light in my greenhouse comes chiefly from one side, not vertically downwards, and yet *Antiopa* usually rests with its head pointed straight downward with the axis of the body vertical. The presumption is strong that gravity rather than light is a determining cause.

To test the phototropic factor, I covered the cage with black cloth and arranged a mirror so that illumination was exclusively from below. One entirely satisfactory test, with a mirror, tended to support the theory that light is effective in determining the posture, for I once found the individuals on the vertical walls, all resting head-up, turned directly or obliquely away from the source of light. This is in striking contrast with the head-downward position which is usually observed even when the top of the cage is covered with black cloth. The experiment should be repeated on a larger scale.

Observations on the antiopas as they grew older and feebler threw new light on the problem. Owing to the atrophy of their fore-legs (as in all Nymphalids) they have more and more difficulty as they become advanced in age in holding themselves head upward on a vertical surface; their center of gravity is too high, so they swing around into the much more stable head-downward position.

Owing to this peculiar head-downward posture, which is evidently connected with the *lack of functional fore legs*, *Antiopa* has become adapted *when at rest on tree trunks* to light rays striking it from above and behind. Accordingly, after alighting on the ground, as well as when resting on a tree trunk, it turns tail toward the source of light, as Parker observed, though it always tends to creep and to fly toward a moderately strong light. Thus the apparent paradox of a positively phototropic insect facing away from the source of light when at rest is more clearly understood. This butterfly is adapted to receiving light from behind, an adaptation which begins even in the chrysalis, for the butterflies which have been observed to turn the head away from the source of light upon alighting are Nymphalidae and, as chrysalids, are suspended head downward. It is probably too early to say that all Nymphalids behave in this fashion, but I have recently had the opportunity of observing in the bright sunlight of the Mediterranean coast two common Nymphalids, *Pararge egeria* and *Vanessa cardui*, which regularly turn away from the source of light upon alighting, lowering their wings to a horizontal position.

GEOTROPISM IN COLIAS

A striking peculiarity of *Colias philodice* and *C. eurytheme*, in which they differ from *Vanessa antiopa*, is their positive geotropism in darkness. When a cage full of *C. philodice* and *C. eurytheme* flying actively in sunlight and at a high tempera-

ture is carried into a dark room, their activity continues for a minute or two. They do not fly upward as Parker has observed *Antiopa* to do in a dark room, but violently downward, repeatedly striking the bottom of the cage. The noise produced as they hit the floor in their hopping flight reminds one of a popper full of snapping corn over a bed of hot coal.

An unconfined butterfly of this genus in a weak light no longer flies upward but downward. It jumps or flutters at random about the floor of the room, or upon the ground, and soon comes to rest. Females which have begun to lay actively, especially if also old and feeble, fly very close to the ground.

PHOTOTROPISM

Light and heat have the most powerful control over the activities of diurnal Lepidoptera. Increase in light and heat, up to a very high intensity, stimulates activity. Bringing a cageful from darkness into strong light does not, however, produce an immediate reaction. A period of adjustment of about a half minute in *Colias* is necessary before activity starts and the butterflies begin to hover at the top of the cage.

When attuned to daylight, as they are in the fields, sudden increase of light, due to the floating away of a cloud, produces an outburst of activity and, if internal physiological conditions concur, the butterflies soar far upward. An oncoming cloud, if it cuts off much light, will send every butterfly to cover, though individuals, and especially species, differ greatly in this respect.

TILTING POSTURE WHEN RESTING IN SUNLIGHT

If a cageful of *Colias philodice* is brought into the slanting rays of the morning or late afternoon light (about 45° above the horizon), those resting on the floor of the cage often *tilt* the body and folded wings away from the source of light. The rays strike at right angles the exposed surface of the wings. Resting butterflies remind one of the leaves of plants which slowly turn themselves into a similar position in respect to the sun's rays, so that the whole exposed surface is evenly illuminated (fig. A). If a tilting butterfly resting on the ground is picked up and turned around 180° on the same plane, so that it now faces in the opposite direction, it will again tilt away from the light, though this time the other side of the body and under surface of the wings of the other side are exposed to direct sunlight.

This adjustment is made by the flexure and extension of the legs, as described by Garrey (1918) in the robber fly, except that this fly leans toward, rather than away from, the source of light.

Previous writers have not taken account of a possible sensitiveness of the wings to radiant energy (heat rays probably). If we should assume that in both cases the insect tilts itself until the wing surface is evenly illuminated, the apparent contradiction between the two insects would disappear. The robber fly's wings are, of course, held horizontally over its back instead of vertically. Accordingly, it leans *toward* rays coming obliquely (45° above the horizon), while the butterfly with wings closed above its back when resting on the ground, leans *away* from the source of light. In both cases, the light waves strike the plane of the wings at right angles.

But this idea does not take into account the fact that the compound eye is certainly involved. A robber fly with the lower part of its eyes covered, stretches upward; with the upper part covered, it crouches upon the ground; it leans toward

light striking its eyes sidewise. Its body and eyes stretch toward the light. The butterfly, on the contrary, if resting on the ground, rolls over on its long axis, away from the light. This might be described as negative phototropism when at rest and the matter dismissed, but it is

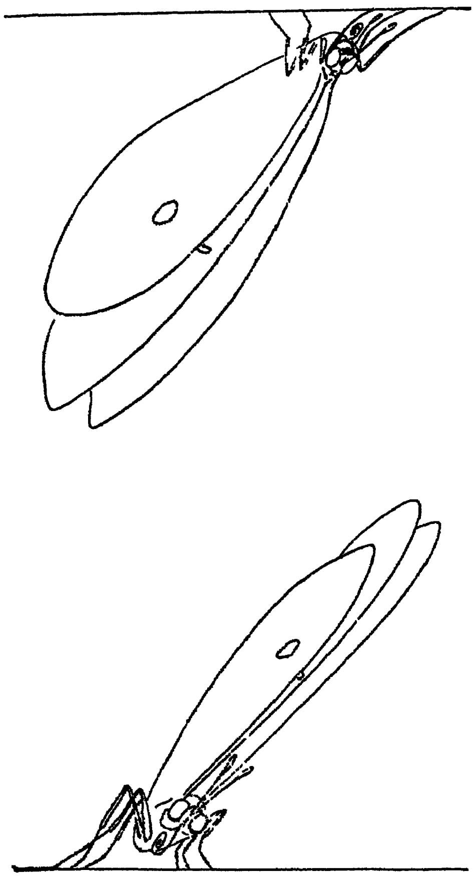

FIG. A. POSTURE OF BUTTERFLIES OF THE GENUS *Colias* IN RESPONSE TO DIRECT RAYS OF SUNLIGHT

not so simple as that, for I have often observed in a cage containing many butterflies (*Colias philodice* and *C. eurytheme*) and in which the light was coming through the netting obliquely from above, that those clinging to the top of the cage, with furled wings and back turned downward, tilt, like the robber fly, *toward* the source of light, while others resting on the bottom of the same cage are tilting *away from* the light (fig. A). In both positions the plane of the furled wings is perpendicular to the slanting rays of the sun; all parts are equally illuminated, like the leaf turned broadside to the light.

It is, of course, highly probable that the eyes are involved in this adjustment. One may imagine that the central facets, *i.e.*, ommatidia, may be more sensitive to light received from stationary objects and adapted for use when the butterfly is at rest, while the other parts of the eye are sensitive to light from moving objects which tend to disturb the repose of the insect. Possibly the latter are connected more directly with motor nerves, the former with nerves which inhibit muscular action. There is, however, the possibility that the wing surface itself is sensitive to light or heat waves, and that, just as the mourning-cloak butterfly rests with the upper surfaces of its expanded wings fully exposed to the direct rays and its head turned away, as Parker has described, so in *Colias* and other butterflies which close their wings we may have a reaction in which sensory impulses from the wings supplement those from the eyes. One certainly gets that impression in watching groups of listing butterflies resting on the moist ground out-of-doors on a summer morning.

Recently on the Riviera I had the opportunity of observing eleven individuals of the green hairstreak, *Callophrys rubi*, sprinkled over a lavender plant in full bloom, each with wings closed above its back and each listing at right angles to the sun's rays except when momentarily changing position during feeding. Thus certain Lycænidæ, like certain Pieridæ, list in the sunlight, unlike those Nymphalidæ which, upon alighting, turn away from the light and open their wings so

that the upper surface is exposed to the direct rays of sunlight.

FEEDING

A butterfly does not deliberately seek food. If the weather is cold and cloudy, it does not feed at all except that, when sufficiently stimulated by an increase in temperature or intensity of light, it extends its tongue to take moisture from the object on which it rests. The flying butterfly, controlled enormously by light rays, gets its food in a very casual fashion. The flower presents a bright reflecting surface on which it alights; then the moist, warm surface brings about the extension of the tongue and the rest of the feeding reflex. The moist surface of the hand or of the ground, certain flowers, like phlox and clover, are almost certain to make the tongue extend. Other flowers, particularly the geranium, have an inhibitory effect, or none at all.

Thus smell probably has a stimulating or inhibiting effect supplementary to light, in controlling feeding in the butterfly, whereas the nocturnal moth depends still more largely upon smell in finding and taking food, as it does in mating.

MATING

Mating in butterflies takes place in bright sunlight or at high temperature, but a sudden increase in intensity of light or heat sometimes brings it about in comparatively weak daylight and cool weather.

In the field, coupling often occurs during flight, and the male sometimes carries the female a considerable distance before alighting. Individuals ready to mate are unusually active. The female flutters with depressed wings and upturned abdomen. The male approaches from the side when the female is in flight or clinging to a plant or other object, presents his abdomen, and union suddenly occurs by the action of the male's clasps and hook. Then the female drops passively, and hangs attached to the male, facing in the opposite direction. The hind wings of the male overlap and half-conceal the hind wings of the female. He supports her weight in flying. When they are standing on a horizontal surface, he drags her about, while she loosens her foothold and allows herself to be pulled. If one holds the male by the costal margins of the forewings, the female remains passive, but if, on the contrary, the female is held, the male never hangs limp but swings round to get a foothold on one's finger or flutters violently.

Mating lasts usually about an hour, varying from about fifteen minutes to several hours. In my breeding experiments it has sometimes been necessary to pull members of a pair apart to prevent their remaining attached together indefinitely.

One coupling is sufficient for a female's whole lifetime. It rarely happens that a few infertile eggs are laid late in life. In the field a female may probably mate with several males successively, and any wild female may be confidently expected to be fertile. Mating occurs in *Colias* as soon after eclosion as the wings are dry. I have frequently brought about successive matings of a single male with three or four females.

EGG-LAYING

The flight of a female is always controlled largely by light, but as she grows older she gradually loses her strong instinct to fly upward and tends to settle upon the bright reflecting surfaces of the leaves to deposit her eggs. The touch of her feet upon the surface of a leaf and the odor of her special food plant causes the flexion of the abdomen. *Colias philodice* alights

on the sunward side of the potted clover plant with her back to the light, crawls to the summit of the leaf, bends her abdomen till it touches a flat surface and then deposits the egg. In *Colias* it is a spindle-shaped egg standing upon end, stuck to the leaf by the secretion of the cement gland acquired as it passes out of the oviduct. It is interesting to grasp an actively laying female by the front margins of the fore-wings and, with her coöperation, place eggs where you will on well-chosen leaves, distributing them with a view to providing plenty of clean food for the little caterpillars when the eggs are hatched. It is like using a rubberstamp, a delicate planting machine. In this way, the whole output of eggs may be increased and disease from overcrowding avoided. Crowding frequently occurs if a caged female is inactive and lays repeatedly on the same leaf. If active, she usually takes flight after each egg is laid, and so distributes the eggs somewhat widely.

ACTION OF LIGHT ON THE COLOR OF CHRYSALIDS

It is well known that Poulton in his "Colours of Animals" has described his extensive and interesting experiments showing that in *Vanessa urticæ* and *V. io* yellow and golden chrysalids are produced if the full-grown caterpillar, after it has stopped feeding, come to rest, and begun to spin its silken attachments, is placed in a yellow-lined box under a yellow screen; whereas caterpillars of the same brood, under blue rays, develop into dark colored chrysalids. Similarly in *Pieris brassicæ* and *P. rapæ*, yellow rays were found to favor the production of green pupæ, blue rays of dark gray pupæ marked with black spots. Other species are similarly responsive, e.g., *Vanessa atalanta*, like the other Vanessids, and *Papilio nireus* of Africa, which is particularly susceptible to changes in the quality of the light.

Poulton for convenience divided the period in the life of a full-grown caterpillar, after it has ceased to feed, into three stages: (1) *wandering*, (2) resting in one place preparatory to spinning its silken supports, (3) *fixed*. The period of susceptibility to the action of light was proved experimentally to be during stage (2) and the beginning of (3), that is, while resting preparatory to spinning and immediately after it.

Poulton entertained the idea suggested by Mendola (1893) that the light might produce its effects through the eyes, so he covered the ocelli of caterpillars of *Vanessa urticæ* with black varnish, but found that the pupæ were unaffected by the blindfolding, contrary, as we shall see, to the recent results of Brecher. The experiments of Fräulein Dr. Brecher on these two genera have been most thorough and have gone far toward a physico-chemical explanation of the phenomena.

Two pigments, green and black, are found in the chrysalis; the white color seen in the hypodermis and cuticle probably being a structural effect. The green, soluble in ether, alcohol and petroleum-ether, is called by Przibram and Brecher (1919) a lipochrome (fat-color), the term commonly applied to yellow carotinoid pigments associated with fats in animals. Its composition has not been determined. Whether it is identical with the apparently chlorophyl-derived green in *Colias*, which is not light-sensitive, is in my opinion doubtful. Przibram (1913) designates as "Tiergrün," a great variety of green animal pigments which, he holds, have no relation to chlorophyl, and it is extremely probable that some of them have not. In the Orthoptera, for

example, in which the blood is not green and some of which like *Carausus morosus* are said to develop their green coloration on an exclusively carnivorous diet, there is no reason to suppose that the green pigment is a slightly modified product of chlorophyl. Brecher (1917, 1921b) holds the same to be true of the green pigment in *Pieris*, regarding it as probably the product of the action of an enzyme.

The black pigment is known to be due to the action of an enzyme in the blood, designated as tyrosinase, upon tyrosin produced by the breaking down of proteins. Variations in melanic coloration depend upon the strength of the action of the enzyme. Thus Brecher (1917) found the tyrosinase in the blood of green pupæ less active than in that of the dark. The blood of whitish pupæ contains a tyrosinase which has the peculiarity of turning tyrosin red before becoming black, differing from the blood of all other color varieties, in which the reaction shows a preliminary violet.

The effect of light upon the tyrosinase was shown by experiments *in vitro*. The tyrosinase in blood drawn from caterpillars during the critical period and exposed for four days to yellow rays became less active; while on the contrary that exposed to ultra-violet rays became very active (1921a). The results of these experiments *in vitro*, however, are somewhat less convincing when we find that under other conditions (tyrosinase from agaricus and other periods of exposure) exactly opposite results were obtained (Przibram and Brecher, 1919); exposure of tyrosinase to yellow light increased its activity. In the *in vitro* experiments, moreover, the blood was first precipitated by ammonium sulphate and the precipitate dissolved in a n/80 NaOH solution. Untreated caterpillar blood normally turns black a few minutes after exposure to the air.

Brecher at first believed that the activity of the tyrosinase depended upon variations in its acidity, increased acidity destroying its efficiency. Yellow light accordingly was supposed to increase the acidity, ultra-violet to favor alkalinity. Her recent experiments (Brecher, 1925), however, carried on with great care by delicate methods, showed that the H-ion concentration of the blood of caterpillars and pupæ of *Pieris brassicæ* in different periods of life and when exposed to light rays of different wave lengths is always *remarkably constant*. It has a weakly acid reaction, a pH of 6.6 (6.50–6.77). Fink (1925) in *Pieris rapæ* found greater variation at different stages: 6.4 for young larvae, 6.2 in mature larvae, 5.9 for early pupal stages, 6.4 for the late pupal stage, but how extensive were his data and whether they have any bearing upon the action of light do not yet appear.

We are thus still without perfectly satisfactory proof that the activity of tyrosinase in butterfly blood is conditioned by the action of light, but the evidence furnished by Brecher points in that direction. Ultra-violet rays seem not to affect it; they promote rather than retard the action of tyrosinase upon tyrosin during the sensitive period of larval life when internal metamorphic changes are most rapid. Yellow rays prevent the melanic reaction and allow green pigmentation to develop. Whether an enzyme exists which promotes the formation of green pigment or whether the variable green is a highly modified derivative of chlorophyl are questions which we cannot yet answer.

The question was raised by Mendola (1873) and by Poulton (1887) whether these pupal color adaptations were produced through the eyes and nerves or by the direct action of the light upon the skin of the larva. Poulton (1887) covered the eyes of caterpillars with black varnish just previous to the sensitive period and

got negative results, leading him to believe that the light acts directly on the skin, not through the eyes. But Przibram (1922) found that by cauterizing the eyes or cutting off the whole head he got the same results as in darkness, whatever the surroundings, that is, the action of the light upon the skin is indirect and through the eyes. Brecher (1924a) similarly found that by coating the ocelli of the caterpillars with transparent yellow varnish, the pupæ became green in *Pieris brassicæ*, golden in the Vanessidæ; when blue varnish was used dark pupæ were the result, as when the insect is kept in blue surroundings. When yellow or blue varnish was used, the nature of the surrounding light became a matter of indifference. The light of long and of short wave lengths thus exerts a differential action only through the ocelli of the mature caterpillar and apparently by nervous control, rather than by direct action through the skin; the mechanism of this nervous control is still unknown.

Dürken (1923) studying *Pieris brassicæ* came to similar conclusions as regards the effect of orange light in preventing the development of black and white pigments, thus allowing the yellow-green pigment to become evident. He found, moreover, that the green color acquired by pupation in orange light, was transmitted to the next generation when pupating in non-colored surroundings; only 7 per cent of a normal control culture pupating in colored environment were green, 93 per cent white and black. The effect of having exposed the parents to orange light was greatly to raise this proportion of 7 per cent. This effect, moreover, was cumulative, for after two generations of exposure to orange light practically every individual descendant, pupating under normal non-colored conditions of illumination, was green. The hereditary transmission of the green (which is essentially the suspension of the melanic reaction) is described as plasmogenetic, or "hologenetic plasmatic induction." The plasma or cytosome of the green cell is affected but not the nucleus.

An objection which might be raised to these experiments of Dürken is that they were mass cultures. The progeny of individual females were not segregated but considered *en masse*, but it is doubtful if more exact methods would have changed the general result.

LIGHT AND WING COLORATION

Little is known about the morphogenetic or physico-chemical effects of light upon wing coloration. Negative results were obtained by Standfuss (1896); Weismann (1895); Kathariner (1900, 1901). Von Linden (1899) observed that *Vanessa urticæ* and *V. io* raised under red glass were in general brighter than the others; those under green, darker; those under blue, paler.

Cholodkovsky (1901) described three aberrant specimens of *V. urticæ* which he obtained out of about fifty bred under yellow or under blue glass. The two bred under blue glass showed an incomplete development of the scales of the hind wings (in one case elongated and hair-like, similar to those of the posterior margin). One could easily pick out of a large series of *Colias eurytheme* or *C. philodice* diseased specimens which show a similar incomplete development. The other aberration, bred under yellow glass, was evidently a melanic, healthy individual with certain spots suppressed; but there is no evidence whatever that it would not have appeared if it had been raised in normal white light.

The general objection which must be raised to all such experiments which do not rule out, or take into consideration,

hereditary factors is that they prove nothing. Large broods of butterflies, especially if inbreeding has been going on, frequently provide aberrations which are seized upon by the experimenter in search of variations as results of external influences; whereas they are due to the interaction or mutation of hereditary factors.

Experimentation should take a new direction and rule out hereditary factors. This can be done, in study of direct action on the wing, by unilateral treatment, exposing to the light to be tested one side of the body only, leaving the other as a control. When one remembers that in certain localities in South America the butterflies of different groups resemble one another surprisingly in their hue, so that as the traveller passes from one region to another he comes upon characteristic local types of coloration, the possibility of light playing some rôle along with food and moisture in the hæmal or cytoplasmic control of development deserves study. We have too long been content with explanations of these interesting phenomena by natural selection. However well or poorly this theory is supported by facts, it tells us nothing of the metabolic processes, the physiological responses of the living organisms with which we are working, to which primarily we must look to learn why and how specific forms and colors are what they have become.

Preliminary to this experimentation one must inform himself about the nature of structural, as well as pigmental colorations. An important contribution to the morphology of structural colors has been made by Süffert (1924), who has described the scales of the butterfly's wing with great thoroughness, amplifying and at some points correcting the work of Onslow (1923) and earlier writers.

ACTION OF TEMPERATURE. SEASONAL CHANGES IN COLORATION

The rate and the extent of the various processes of butterfly metabolism, as expressed in coloration of caterpillar or chrysalis or butterfly, are strikingly under the control of temperature. Coöperating, however, with low temperature, as winter approaches in high latitudes, are weakened illumination and the shorter day. Reduced heat and light stunt growth, diminish the brilliance of certain colors and, within certain limits, promote the development of melanic pigmentation. Moreover, the whole mechanism may come to a standstill, feeding cease, the heart beat rarely or not at all, when the caterpillar, pupa, or adult goes into hibernation.

It is well-known that true melanism is the result of the oxidation of certain products of katabolism (tyrosin, dioxyphenylalinine = "dopa") through the action of one or more ferments, e.g., tyrosinase, and that this action depends very much upon temperature. A high temperature (80°C. for example) destroys the tyrosinase *in vitro*, whereas moderate cold (e.g., 10°C.) favors its action.

The statement that melanism is brought about by a certain degree of cold, corresponding to out-door temperature of autumn or early spring in north temperate latitudes, needs qualification by emphasizing the fact that not all black pigments of butterflies are physiologically alike or, probably, chemically alike. The black variety, "*glaucus*," of *Papilio turnus*, the common yellow swallow-tail of the United States is, as is well-known, found only in the warmer southern states. Cold can have nothing to do with its origin. Similarly, in the classical example of seasonal polymorphism in

Europe, *Araschnia levana-prorsa*, the dark-brown, almost black, variety occurs in the summer generation.

New light has been thrown on this case of seasonal polymorphism by recent studies of Fritz Süffert (1924), who draws a distinction between the physiological effect produced when individuals of the summer generation, which should normally become the very dark *prorsa*, are acted upon by cold as caterpillars or, on the other hand, as chrysalids. In either case the results are similar, that is, a large proportion become the reddish-yellow spring form *levana* or intermediates, and the stimulus, lower temperature, is the same; but when *caterpillars* are treated, the whole course of development is retarded and prolonged ("latent Entwicklung" of Weismann), whereas *chrysalids*, after refrigeration and the return to normal temperature, continue their development at normal velocity ("subitane-Entwicklung" of Weismann). In the latter case we have merely local action upon substances concerned with wing coloration; in the former a general effect upon the rate of metabolism of the whole body.

Süffert has found that the period of susceptibility of the *pupa* to cold is limited to the first twenty-four hours after pupation, and that the susceptible period for the hind wings is in advance of that for the fore wings (maximum effect at twelve hours rather than twenty-four).

Süffert holds, as did Weismann, that it is not low temperature primarily which turns the progeny of *prorsa* into *levana*, for *hibernating* pupæ invariably produce the spring form, *levana*, even when kept in a *warm room* and, so far as known, even when the chrysalis is exposed to heat during the period of susceptibility. Cold affects primarily the rate of metabolism and development rather than the chemical elaboration of pigments. Heat applied to offspring of the summer generation forces on development, resulting in a large proportion of *prorsa* which eclose before winter and within a few weeks.

Süffert's experiments show that the extent of modification of *prorsa* into *levana* depends upon the velocity of individual development, as indicated by the time of eclosion; the slower the individual development the greater is the modification into *levana*. For example, mature caterpillars were exposed to +5°C. during the last days before pupation and after pupation *immediately* brought into a warm room at about 20°C. The sensitive period of the *chrysalis* was thus passed in the warm room, but nevertheless a few *levana*-like individuals appeared among those not modified, and in the following order. The first butterflies to appear were normal *prorsa;* the rest eclosed 1, 2, 3, and up to 8 days afterward, and the later they eclosed the more were they like *levana*. Some individuals indeed did not eclose the same season, their development becoming completely "latent," using Weismann's term for the tendency to hibernate. The others were "incompletely latent" and in varying degree. It remains to be proved whether a hereditary rhythm exists, that is, if climatic conditions were exactly stable, there would still be an alternation in successive generations.

Almost as much difference occurs between the seasonal varieties which succeed one another in the *alfalfa* butterfly, *Colias eurytheme*, of Western and Central United States as in *Araschnia levana-prorsa*, though in the former the color pattern is unaffected. But an extraordinary difference in size occurs between the spring variety, *ariadne*, and *amphidusa* (or *eurytheme* proper) of the summer. The autumn brood, growing while the days are becoming cooler and shorter, is intermediate, and is called var. *keewaydin*. The

changes in coloration consist in the different degrees of elaboration of orange pigment in the yellow scales providing the ground color of the upper sides of the wings. In the little *ariadne* the orange is much paler than in the large brilliant *amphidusa*, this difference being more striking in the male, which is always more highly colored, than in the female. It has usually been assumed from Hopkins' (1895) studies on the yellow pigments of Pieridæ that they are all purine products, though it should be remembered that the color of the various well-known compounds of uric acid is white. The chemical nature of the orange pigment, and of the orange reaction induced in the blood flowing into the scales of the wing bud at midsummer temperature, are matters deserving further investigation.

The melanic pigmentation of individual scales of the under sides of the hind wings and tips of the fore wings varies inversely with the orange of the upper surfaces, that is, in the summer brood this melanic pigment does not appear except in rare strains in which it is under the control of hereditary factors. Thus, from four brother-sister matings of *philodice* made during the first week in June, 1920, four families eclosed in July, all bred under the same conditions as to temperature. Broods ι, λ, ο were hereditarily swarthy, whereas s was a large brood of 245 adults of typical summer coloration. Brood ι consisted of 253, λ of 133, ο of 281 individuals. No quantitative study in these three broods of the individual variation in melanism, which is considerable, has yet been made, but as a whole these broods are very conspicuously melanic as compared with brood s.

It was for a time my belief that the width of the black wing-border of the male of *Colias philodice* and *C. eurytheme* is narrower in the fall generation. Families raised in the fall have in many cases been characterized by extraordinarily narrow marginal bands, and it is difficult to determine by mere inspection and comparison with the male parent that this is not in part a seasonal effect, the width of the band being subject to much individual variation; but the corresponding females do not show a proportional narrowing of their marginal band. The width of the band is certainly in general inheritable, and the fall broods showing exceptionally narrow bands were produced by close inbreeding, so that I must conclude, until careful quantitative studies have been made, that the melanic border of the upper side of the wings is not essentially affected by heat and cold.

It is especially the under side of the wings of butterflies, as, for example, in the small blue Lycænid, *Pseudargiolus lucia-neglecta*, which is particularly subject to seasonal changes in melanism. The oxidation taking place in the tyrosin-tyrosinase reaction and the production of melanism is promoted by the exceeding thinness of the membranous diaphragm separating the scales of the under side of the wing from the underlying air cavity, thus allowing the air to come into close contact with the scales. The cuticle of the wing bud immediately covering the upper surface of the fore wing, however, is much thicker and probably impervious to oxygen, which accordingly reaches the developing scales of the wing-surface between the nervures only internally through the tracheæ, so that there is less oxidation and less elaboration of melanin on this upper surface, except for those markings of the color pattern which will be described later.

Caterpillars of *Colias eurytheme* show an interesting seasonal melanic variation. In certain strains bred in the fall and winter two dorso-lateral rows of squarish black

spots appear. A pair of them occurs close to the posterior margin of each segment, apparently just over the lateral margin of the pericardium (fig. B).

Nothing is known of their heredity, and since nothing exactly corresponding to them is ever seen in the summer generation it would not be possible to follow the course of their transmission, which may be very irregular like that of the bright-colored dorso-lateral lines in *C. eurytheme* caterpillars, on which I have a series of unpublished data, or like the gray-black and the green larvae of the Elephant

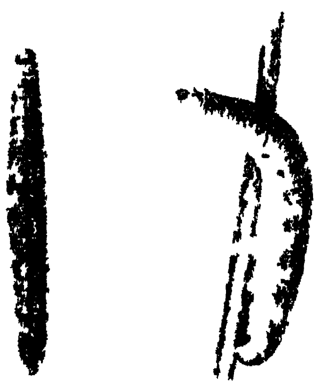

FIG. B. SEASONAL MELANIC VARIATION IN CATERPILLARS OF THE ALFALFA BUTTERFLY *Colias eurytheme*

Black dorso-lateral spots appear only in late fall and winter

hawk moth, *Chaerocampa elpinor*, which Federley (1916) regards as belonging to one biotype, one hereditary pattern.

THE PHYSIOLOGY OF MELANIZATION AND OF A SIMPLE COLOR-PATTERN

The wonderful variety of form and color in the patterns upon the wings of butterflies is so familiar to us and so appealing to our love of the beautiful that it probably seldom occurs to one that each pattern and even the localization of each spot and band has its physiological meaning. But until recently little effort has been made to assign any other meaning to these patterns than that of protection against enemies, chiefly birds, which were thought, and in fact known, to eliminate individuals not especially protected. If a butterfly could be shown in a small minority of cases to resemble a leaf or bark of a tree, or to have an odor faintly disagreeable to mankind, or to resemble another accused of having such an odor, we have been content to think that natural selection would somehow account for color patterns generally. Yet we have always recognized that natural selection, which remains the only theory which we have of the origin of adaptations save the still poorly-supported Lamarckism doctrine of direct environmental action, depends upon variations about the origin of which we have known next to nothing.

It is the recent advances in the study of variations, knowledge of to what extent and how they are inherited, and especially the physico-chemical mechanism of their development in the individual, which are the hopeful signs of progress in the science of evolution. When we can understand by the help of physics, chemistry, embryology and ecology how even the simplest organism takes on the patterns which it assumes during its span of life, we shall have taken the next essential step in the study of evolution.

So it has seemed to me that, in beginning the investigation of the origin of the wing patterns of butterflies, we should choose one that is very simple and which depends upon chemical processes of pigmentation about which something is already known. Such a wing pattern is that of *Colias philodice* and its near relative *Colias eurytheme*, consisting of a simple black border (narrow and unbroken in the male, broader and usually splashed with spots of the yellow ground-color in the female) and a black discal spot in the middle of

RELATION OF CUTICULAR PITS IN THE WING BUD TO THE MELANIC BORDER AND DISCAL SPOT

Figs 1, 2 (Upper left, top row) Mature male pupæ showing blackened pits at the edge of the black border of the underlying wing and close to the black discal spot Figs 3 4 (Upper left second horizontal row) Same in mature female pupæ Fig 5 (Third horizontal row extreme left) Young pupa showing just blackened pits in the cuticula before development of pigmentation in the wing Fig 6 (Fourth horizontal row, lower left corner) Cast pupa case showing blackened cuticular pits Figs 7 10 (Four figures at right) Effect of closing with beeswax the pits in the right wing bud of young pupa Fig 7 (Center of plate) Cast pupa case of a male, showing wax over the pits Fig 8 (Upper right corner) Same male butterfly effect of closing pits on right wing bud of pupa, note small modified right wing shortened 2 5 mm Fig 9 (Bottom row middle) Cast pupa case of a female, wax covered pits Fig 10 (Bottom row right corner) Same female right wing shortened 2 5 mm

each fore wing. What determines the position and extent of these deposits of melanin? Why is the border broad and irregular in the female, narrow and solid in the male?

The clue to the answer to the former question was soon found in the presence of a minute pit in the cuticula at the middle of the pupal wing bud. Its walls blacken almost immediately after pupation. Spreading backward from this point, about a week later, the black discal spot of the wing itself develops beneath the thick but transparent cuticula. Similarly a row of minute cuticular pits, connected usually by a furrow, run parallel to the margin of the wing-bud immediately above the edge of the future wing.

It is from this row of pits, which blacken immediately after pupation before the soft, freshly-secreted cuticula has hardened, that the marginal band of the underlying wing is later to develop, extending inward toward the middle of the wing. The yellow pigment in the scales of the general surface is already formed while the marginal band and discal spot are still in a transparent, colorless stage. Thus the position of the marginal band is determined at an early period, and it was imagined that an exchange of oxygen and carbon-dioxide might be taking place through the pits and extending over the future melanic areas. To test this hypothesis, I blocked the pits of many pupæ with bees-wax immediately after pupation, in some cases before the cuticular pits themselves became blackened. Closure of the pits, however, did not suppress the black marginal band, which developed in all cases normally, but it evidently interfered with metabolism and checked the growth of the wing, so that, in almost every individual, the wing thus treated became shortened, as compared with that of the other side which was left untreated as a control. The oxygen necessary for the melanic reaction must accordingly have come from the thorax through the tracheæ. I am led to think that the pits are respiratory and serve for the escape of carbon dioxide from the following evidence: the blackening of the pits while the cuticula is still soft, the colorless areas of scale-bearing epithelium beneath them where yellow pigment does not form but which eventually blacken, and the stunting of the wing when the pits are closed. Incidentally this throws light on a question which has puzzled students of the physiology of insects, viz., how is carbon-dioxide eliminated.

It is possible, and indeed probable, that the central pit of the pupal wing represents the suppressed spiracle which fails to develop in the mesothorax of the caterpillar, for through the translucent wall of the larval thorax one observes that the line connecting the spiracles crosses the middle of the wing bud. In some individuals a slight depression is visible in the mesothorax at the point where a spiracle ought to be. The suppressed spiracle, involving a cuticular pit permeable to gases, probably determines, therefore, the position of the discal spot in the wing-pattern of the butterfly. The marginal band of the butterfly's wing can similarly be traced back to a submarginal bundle of trachioles in the wing bud of the caterpillar, which corresponds in position to the submarginal row of pits and the connecting furrow in the pupa.

Thus the simple wing pattern of this butterfly probably owes its main features to details in the respiratory system of the caterpillar's wing bud.

There are many unsolved problems about the determination of the wing pattern in *Colias*. How can we explain the greater width and more diffuse inner

margin of the melanic border in the female as compared with that in the male? Experiments looking toward the solution of this and other questions are not yet far enough advanced to be reported at present, but new methods have been devised which promise more accurate knowledge of wing color and pattern.

Onslow (1916) has studied the chemical basis of the black markings on the wings of *Pieris brassicæ*. The immature fore-wings were dissected out of a number of pupæ and placed for twelve hours in watch glasses containing (1) saline solution, (2) hæmolymph (from crushed pupæ ground up with kieselguhr and chloroform water), (3) saturated tyrosin solution.

A wing kept in normal salt solution turns slightly black, but if previously boiled it remains uncolored.

A wing placed in hæmolymph turns black even if previously boiled, but if both wing and hæmolymph are boiled it remains uncolored.

In saturated tyrosin solution a wing turns extremely black, but if a wing is previously boiled it remains uncolored. The conclusion is reached that both the wing and the hæmolymph, respectively, carry both tyrosin and tyrosinase, since blackening occurs when the wing is placed in hæmolymph unless both wing and hæmolymph have been previously boiled. Both chromogen and tyrosinase adhere to the surface of the wing and to the surface of the scales, but whereas white pigment is found (in white areas) on the surface, the black pigment permeates the chitin of the scales. In his general conclusion Onslow holds that the localization of the black area is due to the *restriction of the tyrosin to the black areas*, while the tyrosinase is everywhere present, for when the wing is placed in a tyrosin solution it becomes black all over, but when it is placed in a tyrosinase solution the darkening is restricted to the markings. Thus the form of the markings is determined by the localization of the tyrosin in these areas, and oxidation takes place as soon as the atmospheric oxygen has access to the surface of the wing.

PIGMENTS IN THE BLOOD AND THEIR ORIGIN

Although all butterfly pigments are in last analysis blood pigments, few of them give color to the hæmolymph. Melanin is produced directly in the blood only when the latter is drawn and exposed to oxygen of the atmosphere. The white and yellow wing pigments of the Pierids, usually regarded as products of uric acid since Hopkins (1896) found that they give the murexid test, are deposits left by the blood within or upon the scales. A third group of pigments, possibly derived without much chemical change from food-plants, color the hæmolymph green or yellow.

The best known of these are the yellow carotinoids, which in birds and mammals are associated with fats or lipoids. If leaves of plants and vegetables containing carotin are omitted from the food of a fowl, the yolks of the eggs which she lays become pale, being deprived of the yellow pigment, carotin, which is ordinarily absorbed in digestion of green plants. In certain breeds, e.g., the white leghorn, this pigment appears in the ear lobes and legs, as well as in body fat and blood serum. Since it is gradually used up during egg-laying, the legs of good layers become progressively paler, whereas those of poor layers remain bright yellow. Butter from cows at pasture is bright yellow, from cows deprived of fresh green food it is paler. The yellow pigment of the corpus luteum, body fat, and blood serum in mammals is known to be carotin.

Carotin is a highly unsaturated hydro-

carbon. As extracted from carrots, it has the formula $C_{40}H_{56}$. Xanthophyl is its dioxide, $C_{40}H_{56}O_2$.

Meldola (1873) first suggested the idea that the green color of certain insects is due to the absorption of chlorophyl from the food mass in the intestine, with slight modification, into the hæmolymph.

Poulton (1885, '86a, '86b, '87, '93) in a series of interesting papers made a distinction between those pigments which are formed within the tissues of leaf-eating larvæ ("endogenous," Verne, 1925) and those derived from the food ("exogenous"). "The derived pigments often occur dissolved in the blood, or segregated in the subcuticular tissues (probably the hypodermis cells), or even in the chitinous layer, closely associated with this cuticle itself."

It was clearly brought out by Poulton that the digested pigments undergo extensive and very diverse chemical changes in their absorption into the blood in different caterpillars. They become associated with the proteid of the blood or tissue. When alcohol is added to the hæmolymph of the buff-tip moth, *Pygæra bucephalus*, the proteids are precipitated, carrying with them the chlorophyl which soon disappears, leaving the carotin ("xanthophyll") in solution. Palmer (1922) says of this "If the affinity of carotin for blood protein, as found in some cases for mammals, is a universal property of this pigment, these results of Poulton's on the hæmolymph of caterpillars lend support to the tentative conclusion that the chief carotinoid of the larvæ and pupæ of butterflies is carotin."

The view that the green and yellow blood pigments of certain green caterpillars are derived from chlorophyl and carotin of their food, though very generally held, has not been adopted by Przibram and Brecher. Przibram (1913) found that, by heating the ether solution of the pigments of certain green animals (green grasshoppers, *Cantharides*, the frog) with an equal quantity of alcoholic solution of potassium hydroxide, a yellow precipitate is formed and the solution becomes clear, in contrast to the extract of plant pigment, which remains green and turbid. Upon application of more potassium hydroxide and heat, a still more striking difference appears: the extract of animal pigment remains clear after the formation of colored precipitates while that of the plant pigment remains cloudy and contains a black precipitate. Concentrated sulphuric acid applied to the ether solution of "animal green" gives a wine-yellow color, becoming brown, whereas the plant extract remains green. Nitric acid decolorizes the animal extract, while that from plants remains green or fades out slightly into yellow.

These reactions are such as one would expect if the various animal pigments are associated with proteins, as they certainly are in the hæmolymph of Lepidoptera, and if those extracted from leaves are relatively free from such albuminous substances. These reactions present no reason for uniting together in one category ("Tiergrün") all green animal pigments nor for claiming that none of them may be a compound derived directly from chlorophyl. No one would imagine that the green pigment of the carnivorous frog, or of the mantis, grasshopper, or, in fact, any of the Orthoptera, can have their immediate source in chlorophyl, but one may hold an entirely different opinion in regard to some of the green pigments in caterpillars. The well-known experiments and observations of Poulton (1885, 1886a, 1886b), point in this direction, especially those on the larvæ of the moth *Tryphæna*, which, after feeding normally on leaves of cabbage containing chloro-

phyl or etiolin become green or brown, but which, deprived of food containing either, and kept alive by feeding on the mid-ribs of cabbage, lack altogether the green and brown pigments of the body wall.

This experiment, however, in my opinion, is not wholly conclusive, though it is perhaps the best experimental evidence which we have that the grass-green pigments of the blood and body-wall of leaf-eating caterpillars are derived from chlorophyl. The principal objections to the experiment as described are that we are not informed that the hæmolymph in *Tryphana* is green or pigmented; the single caterpillar which survived after being deprived of food containing chlorophyl was extremely small (about one-fourth the normal length), its growth being greatly stunted; if the green and brown pigments are truly endogenous, rather than derived from chlorophyl, the stunted growth may have interfered with their development; of the other caterpillars, fed on chlorophyl, only two of the last twenty-three survivors were green, the remaining twenty-one brown. The brown pigment of the body wall is hypodermal, however, and very evidently of a different origin from the typical *cuticular* melanic pigmentation. The further evidence adduced by Poulton (1885, 1886) that chlorophyl is the source of these green and brown pigments rests chiefly on comparisons between the absorption bands in the spectra of the hæmolymph of green caterpillars and of green leaves. A corresponding absorption band occurs at the red end (70–65) and another (around 50) in the green. In the leaf, however, two additional fainter absorption bands occur in the intermediate region (63–61 and 60–57.5) which have no counterparts in the spectra of the hæmolymph exhibited. Poulton's observations bring out of the fact that the problem is complicated with other factors both hereditary and environmental, which coöperate to determine the green and brown pigmentation of caterpillars, acting as he believes, upon the variable raw materials (exogenous pigments) from the food-plant. The larva of *Sphinx ligustri*, for example, is dull-colored if fed on lilac, bright-colored when fed on privet. The argument in favor of derived green pigments seems also somewhat weakened by the case of *Sphinx ocellatus* (Poulton, 1886, p. 169), in which the blood is only faintly tinged, while the body wall is deeply colored. Thus the blood "cannot produce any effect upon the larval appearance until it has been collected in the superficial cells." The blood is regarded as the medium by which the pigment is slowly transferred to the body-wall. "Before pupation the pigments are withdrawn from the cells and are dissolved in the (pupal) blood. . . ." "Such conclusions render it probable that the most complete demonstration of the vegetable origin of the derived pigments will be a matter of great difficulty." Nevertheless, the experiment on *Tryphana* reported several years later was regarded as conclusive.

The evidence in regard to the transfer of carotin of the food plant to animals is more extensive and satisfactory than that in respect to chlorophyl. It has been summarized by Palmer (1922) in his book on "Carotinoids and related pigments." Knight (1923) and Palmer and Knight (1924) have recently reported that the double-eyed soldier bug, *Perillus bioculatus*, owes its yellow and red colors to carotin derived from the blood of the larvæ of the potato beetle (*Leptinotarsa*), which in turn get it from the leaves of the potato plant. Under low temperatures (65°–75°F) a large amount

of this pigment becomes deposited in the body wall, whence red or yellow variations arise; on the other hand, at high temperatures (85°–95°F) large amounts of it are oxidized and destroyed, so that white variations appear in the nymph.

HEREDITARY CONTROL OF A CAROTINOID PIGMENT

An interesting case of the mutations of grass-green into blue-green caterpillars through the action of a simple mendelian recessive factor, which apparently destroyed the normal carotinoid pigment, first appeared in my cultures of *Colias philodice* in August 1920. The stock had descended from a single female butterfly, the progeny of which had wintered as caterpillars. Inbreeding had then occurred for two generations. The caterpillars which hibernated and those of the following (June–July) generation were all of normal grass-green appearance, but in the August generation forty-four conspicuously blue-green individuals appeared in broods containing three times that number of normal larvæ. Evidently the parents of the three particular broods showing this ratio were grass-green heterozygotes for the recessive blue-green factor. Thus one member of the original wild pair of butterflies of the previous autumn must have been heterozygous for the recessive blue-green factor, the other mate being a normal grass-green dominant; and the same sort of combination must have occurred in both of the brother-sister pairs of the spring (early June) generation; their offspring were also all grass-green but 50 per cent were probably heterozygous for blue-green, for from them came the heterozygous butterflies belonging to the summer (late July) brood which, mating together, produced blue-green caterpillars. Other pairs of their brothers and sisters, one or both of which were homozygotes for normal grass-green, produced only grass-green caterpillars.

Unfortunately for the purposes of experimental breeding, the recessive blue-green butterflies, though strong and healthy, seldom would mate together, owing to sterility, especially of the male; however, a mating of this sort was once obtained and blue-green caterpillars only were the result.

The butterflies developed from blue-green caterpillars which survived the winter of 1920–1921 failed as usual to mate, but fortunately several females which wintered as grass-green caterpillars were the offspring of a pair of grass-green parents of which the male was known to be heterozygous for blue-green, for, by another mating, he had produced some blue-green caterpillars. These females, of which one half, though grass-green, were heterozygous for blue-green, were mated early in May with wild males. Inbreeding in one of the families of the second generation (June–July) gave again in August most extraordinary results. In three families another mutation or variety which I had never seen, caterpillars with olive-green skin, appeared with the double dominant grass-green and recessive blue-green in the ratio: 9 grass green, 3 olive, and 4 blue green. Four other matings produced 314 grass-green and 128 olive caterpillars.

Olive when homozygous for the recessive reddening factor b, (which adds a reddish element to the pigment in the hypodermal cells of the larval skin and of the eye, and tinges certain wing scales of the butterfly with orange) breeds true to olive; a pair homozygous for olive but heterozygous for blue-green (a), viz., Aa bb, throw 25 per cent of aa bb, blue-green, olive being the epistatic color. Doubly heterozygous grass-green individuals, Aa Bb, mated together gave the

9:3:4 ratio mentioned above. The "olive" butterflies, unlike the "blue-green" and especially the male of the latter variety, showed no particular signs of sterility, and were strong and healthy. That is, the olive individuals were as easily mated and laid as well as the grass-green individuals of the same cultures.

The physiological and ecological characteristics of these two variations are of unusual interest. In both of them the green eye of the adult butterfly showed a tinge corresponding to skin color of the caterpillar from which it developed, that is, either a bluish-green or a brownish tinge, not as abrupt a variation as in larval skin-color but always present in individuals known to have been in their youth blue-green or brown caterpillars.

The blood of the blue-green caterpillar and butterfly was distinctly blue-green, that of the olive, so far as could be seen, normal grass-green. The absence of yellow pigment from the blue-green blood and from the hypodermis of the caterpillar and compound eye affects in no way the pigments of the scales, which are of an entirely different chemical nature from the yellow pigment missing in the blue-green caterpillar. The scale pigment, tentatively at least, is to be regarded as a derivative of uric acid, the other as carotinoid. On the other hand, the olive factor which reddens the normal yellow-green hypodermal pigment into olive-green (a mixture of yellow-green and red) also reddens the scales upon the under surfaces of the hind wings and tips of the fore wings, changing them into orange. The scales of these particular surfaces, as I have indicated in the discussion of seasonal variations, are exposed to a high degree of oxidation, which would suggest that the olive factor may perhaps be an oxydase and the olive reaction an oxidation.

The egg of the female with blue-green blood is pure white, not cream-white as in the normal female with yellow-green blood. Similarly, the cocoon spun by the hymenopterous parasite *Apanteles flaviconcha* Riley, when it passes its larval existence within the blue-green caterpillar and feeds upon the blue-green blood, is white rather than bright golden-yellow, the latter being the color of cocoons spun by these parasites after living on normal yellow-green blood.

The blue-green mutation illustrates in the clearest possible way throughout the whole life history of the insect the absence of a yellow pigment from the hæmolymph and from the hypodermis. Even the pink line, which in the normal larva is traced more or less distinctly along the middle of the lateral white band running through the stigmata, is absent from the blue-green caterpillar.

The fundamental question is: how is the yellow pigment suppressed so that the blood and skin become blue-green? If the yellow pigment is carotin derived from the clover which serves the caterpillar as food, as seems highly probable, and if the chromosome hypothesis of the physical basis of heredity is in general true, then we are led to think that the nuclei of the intestinal epithelial cells and especially their chromosomes, produce some substance capable of destroying carotin during the digestion and absorption of plant pigments through these cells into the blood. This is a most definite case permitting the identification of a hereditary factor with a relatively simple physico-chemical reaction localized in a definite tissue (intestinal epithelium) but, through the blood, affecting other tissues, especially the hypodermis.

The alternative hypothesis, favored by Przibram, is that the yellow pigment is a

"lipochrome" of unknown chemical nature formed within the hypodermal cells and possibly other cells, from which the blood takes it up.

There can be no doubt about the endogenous origin of the gene or factor for blue-green, the active agent in suppressing the yellow pigment. It appeared spontaneously under normal conditions, except for the close inbreeding, and was transmitted in the simplest mendelian fashion. And until it can be shown that the yellow pigment is not a carotinoid, the former hypothesis is more useful. It is supported by much recent circumstantial evidence in regard to carotinoids cited by Palmer (1922), by Verne (1924) and others.

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GROWTH AND DIFFERENTIATION IN PLANTS

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I. INTRODUCTION

WHEN one sees a plant he may be aware only of some striking characteristic, e.g., size, or color, but if he observes he must become aware not only of its specific characters but of a certain relationship between their shapes, sizes, involutions, intricacies, dispersions, contrasts, and diversities. By some these qualities are regarded as puzzling examples of the mystical methods of nature. Others regard them as the expression of forces acting upon the plastic substratum of life to produce organisms having such definite characters as to give one the opportunity to classify them into related groups, species, families, and so on. Furthermore, these characters are unique in being passed on from one generation to another with the result that each individual reaches maturity through a rather uniform series of processes.

This paper will be devoted to a discussion of some of these processes as well as to the characteristics of the mature organisms.

One of the important features of biological processes is their continuity. The organism of today is the organism of yesterday plus or minus a certain number of molecules of water, carbohydrate, and other material. The changes in composition of the cell are wrought, in large part, by enzymes which bring about hydration, dehydration, oxidation, reduction and like changes. These processes go slowly in comparison with many chemical reactions *in vitro*, and are often reversed, but they play an important part in the development of the organism.

The growth of an organism usually begins at a slow rate, gradually increases for a time, then as the organism approaches maturity it goes more slowly and finally no further increases are perceptible. Many chemical reactions proceed in the same way, especially those in which an autocatalyst is concerned.

Our knowledge of the growth of organisms has been immensely advanced in recent years by the application of quantitative methods to its study. Having found that the increase in size of the organism is an orderly change, it is possible to give mathematical expression to it, analogous to those which express chemical changes. Biologists have not yet settled on the general use of any particular algebraic equation to express this relation, perhaps none yet evolved is adequate for the purpose. Their application has however focussed attention upon the orderly nature of the growth process and makes it more apparent that this process is a manifestation of the energy relationships prevailing in other forms of matter.

II. SOME DYNAMICAL ASPECTS OF GROWTH

The successful application of the Verhulst equation to biological data by Pearl and Reed (1922) has attracted no little

attention. The equation appears to lend itself readily to problems of population and to other statistical enquiries.

$$y = d + \frac{k}{1 + me^{a_1x + a_2x^2 + a_3x^3}}$$

here, y = population at time x; d = total growth attained in all the previous cycles; k = the upper limit of growth, or the value of y at infinite time; m = an arbitrary constant of time.

In my own work I have made frequent use of the equation for autocatalysis which has served admirably to analyse the growth processes of organisms. Other equations may be as good, or better, but one must use the tools at hand until better can be found. We may give attention to the equation as commonly used:

$$\log \frac{x}{A-x} = K\,(t - t_1)$$

in which x is the size of the organism at time t; A is the maximum size attained at maturity; K is a constant; and t_1 is the time at which the organism is half grown, i.e., where $x = \frac{A}{2}$. Those who are interested in the derivation of this equation may consult Robertson (1923).

In another place (Reed, 1924b) I have enumerated a number of organisms for which this equation has been found by trial to express the growth.

The value of K (the specific constant of growth) appears to have reality in the examples which have been studied. We may consider the growth rate of sunflower plants which were arranged for purposes of study into four groups according to their heights at maturity (Reed, 1919). Table 1 shows that the average final heights of plants in the four groups were quite variable, ranging from 198 to 312 cm., though the values of K were remarkably constant. The fact that the mean values of K are within the range of their probable errors may be taken as evidence of a specific velocity constant in the plants of the four groups. The dispersion of the growth constants from their means, as measured by the standard deviations, of the larger plants was wider than that of the smaller plants.

TABLE 1
Height and growth constants of sunflower plants

	QUARTILE			
	I	II	III	IV
Mean final height of plants at maturity	198 cm.	238 cm.	272 cm.	312 cm.
Mean value of K	0.0440 ± 0.0011	0.0421 ± 0.0016	0.0429 ± 0.0017	0.0443 ± 0.0023
Standard deviation of values of K	0.0052 ± 0.0008	0.0079 ± 0.0011	0.0079 ± 0.0012	0.0111 ± 0 0016

If the foregoing assumptions concerning the specific velocity constant are correctly taken there must be something else which determines the final size of the organism. Gaines and Nevens (1925) have made the interesting suggestion that A/K is a specific constant representing final "growth capacity." Its value as an index of growth capacity depends upon the association between the length of time that the crop, or one of its constituents, continues to grow, and the final extent of growth. This obviously ought to follow and the authors found evidence for the correctness of the assumption with the plants they studied.

A brief experience with growth curves of organisms will show that cylic or periodic growth is common. In man there are three post-natal cycles of growth, infantile, juvenile and adolescent. These cycles overlap to some extent and it is often impossible to discern their exact limits. Indeed, the more we know about them the less reason we have to expect that they have any well marked boundaries. The quantitative treatment of these cycles presents certain problems, but none are necessarily insoluble.

The existence of intra-seasonal cycles of growth in the shoots of certain trees, has been shown to be quite independent of definite fluctuations in environmental conditions. A more extended inquiry will undoubtedly show many cases of cyclic growth in plants. Laughlin's (1919) quantitative studies on the periodicity of cell divisions in onion root tips point the way to fruitful investigations.

TABLE 2

Comparison of the constants of the curves for intra-seasonal cycles of growth of apricot shoots

	CYCLE		
	I	II	III
K	0.0380	0.0355	0.0277
k	0.000344	0.000509	0.000605
$\frac{A}{K}$	2895	1964	1653

The measurement of a population of shoots on young apricot trees (Reed, 1920a) showed three definite cycles of growth, each conforming to the type of growth curve above discussed.

The first cycle covered the period from 0 to 8 weeks, the second from 9 to 17 weeks, and the third from 18 to 28 weeks, dating time from April 20. The values of A for the three cycles were taken as 110.4, 69.7, and 45.8 cm.

The correspondence of observed and calculated values was satisfactory in each cycle. The values of the growth constant K showed comparatively little variability in the three cycles, but those of k were less constant, (table 2). The progressive decline in the values of $\frac{A}{K}$ may indicate, as Gaines and Nevens (1925) have suggested, a progressive lowering of the growth capacity of the shoots.

There seems to be little chance for doubt that these fluctuations in the rate of elongation have a real physiological significance. Certain aspects of this problem have already been published (Reed, 1921a) in which I showed that sap concentration and growth seemed to be inversely related. When growth was rapid the concentration (measured by the freezing point depression) was less, and *vice versa*. Expressed in the form of a coefficient of correlation I obtained values of r approximating -0.600.

Reverting to the nature of the growth process in this population of apricot shoots, it seemed worth while to consider another form of growth curve and its mathematical expression. There is a possibility that their growth in length followed the course of a reaction which consisted of two consecutive monomolecular reactions, one of which at first accelerated and later retarded the other. Wilhelmy's equation formed the basis of the attempt from which the equation for the curve was worked out:

$$x = 210\,[1 - e^{-0.095(t-1)}] + 19.1[e^{-0.055t} \cos \frac{\pi}{14} t]$$

This was considered to show that the main reaction (expressed by the first term) was periodically accelerated and retarded by another term (expressed as a function of t involving the cosine). While the assumptions made cannot be pushed too far with the data now avail-

able, it does seem apparent that the cycles of growth had a real existence and that they may be studied as *processes* of some sort.

Additional information was obtained from a study of data on the growth of white rats, which recovered from suppressed growth due to prolonged fasts. Curiously enough, these small starved rats, when given an adequate diet grew to maturity and equalled in size those which had been given adequate diets from weaning (Reed, 1921c). The second cycle of growth of rats recovering from starvation began, and reached its maximum relatively earlier than in the case of rats given adequate diet continuously. Indeed, an equivalent gain in weight was made more quickly in the animals recovering from suppression than in animals on adequate diets.

The existence of cycles of growth may be inferred from the definite way in which laterals are often grouped on the main axis of plants. On a subsequent page there is a discussion of the pattern of young apricot shoots in which it is shown that the size relationships of the primary laterals suggest a distribution in conformity with a curve of cyclic growth. Although this particular instance deals with the static rather than with the dynamic aspects of the problem, the results are compatible with the preceding discussion and justify the assumption that there is a common principle acting in the two instances.

In the light of the evidence briefly presented, showing that there seems to be an orderly, definite growth process resembling in many ways an autocatalytic reaction, it seems logical to discuss the question of growth-promoting substances.

The effect of diffusible substances which have definite growth-promoting abilities may be demonstrated in cases of cell division which follow the isolation of pieces of tissue. A small fragment of tissue containing fibrovascular bundles accelerates the process of cell growth and division. Lamprecht (1918) cut small pieces of leaf tissue (3 x 3 mm.) and placed them upon each other in Petri dishes containing moist sand. Cell divisions occurred only in pieces which contained vascular bundles. However, if pieces with and without bundles were placed one on top of the other, tangential cell divisions did occur, first in the immediate neighborhood of the bundle, later over the entire wound surface. In all experiments the presence of vascular bundles was necessary for the appearance of cell divisions. In the vicinity of the leptome the divisions started first and were more numerous than in the vicinity of the hadrome. The substance which stimulated cell division is not strictly specific, but works between related genera, but not between distantly related genera or families.

The growth promoting activity of the tip of the coleoptile has been shown by a series of decapitation experiments. Söding (1923) cut pieces 3 to 5 mm. in length from the coleoptile tips and accurately measured the length of the remaining organ. The apical pieces were then replaced on certain decapitated stumps and their lengths measured several hours later. It was evident that the replacement of the tips materially accelerated the growth of the coleoptiles and Söding regards the results as evidence that some sort of a growth promoting hormone is produced in the tip which is transferred to the stump by diffusion.

III. STATIC ASPECTS OF GROWTH OF THE PLANT

1. Correlation between age and relative size

Although the growth process has been shown to represent an increase in mass

which is some sort of a function of time, it fails to answer many questions which are of paramount importance in formulating an exact idea of the development of individuals.

If one notes the variability exhibited by a population of plants, especially in a case where growth has ceased, he may properly raise the question of their relative sizes at earlier stages in their development. For example, are the plants which are small at maturity, those which were small from the beginning, and those which are large at maturity likewise superior plants from early life? The question is important not only from a theoretical but also from a practical standpoint. There are several ways of attacking the problem though few biologists have undertaken it.

There is a tendency, especially among those who are unfamiliar with the quantitative investigation of biological problems, to ascribe these differences to the heterogeneity of the environment. That the environment is variable we must admit, yet, after making all due allowance for this cause, there are permanent differences which can only be satisfactorily explained by assuming that they are in some way bound up with the genetical constitution of the plant.

The first and most important work on this problem was that of Pearl and Surface (1915) who investigated the height variations of a population of maize plants during the growing season. Several years later the writer (1919) made a similar study on a population of sunflower (*Helianthus*) plants and obtained confirmatory results. In both studies the height of the plants was measured either semi-weekly or weekly from a very early stage until increase in height ceased. The measurements were assembled so that the plants on each day of measurement fell into quintiles or quartiles.

There was a strong tendency for plants to remain in or near the quintile (or quartile) in which they started. The quantitative expression of this tendency may be derived from a few relatively simple computations. I shall illustrate by use of the data on *Helianthus*. If the quartile positions of the plants at each measurement had been due to the operation of purely random factors, we should expect to have found them in one quartile as often as in another. The theoretical

TABLE 3

Helianthus annuus. Number and percentage of the height measurements which fell in the several quartiles after the original classification into quartiles

QUARTILE IN WHICH PLANTS STARTED	QUARTILE POSITIONS OBSERVED DURING GROWTH OF PLANTS								TOTAL NUMBER	THEORETICAL STANDARD DEVIATIONS	OBSERVED STANDARD DEVIATIONS
	I		II		III		IV				
	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent			
I	68	45.33	31	20.67	28	18 67	23	15.33	150	3.53	11.92
II	26	18.57	52	37.14	35	25.00	27	19.29	140	3.64	7 52
III	42	28.00	36	24.00	47	31 33	25	16.67	150	3.59	4 94
IV	11	7.86	23	16.43	41	29.29	65	46.43	140	3.63	14 60
Total..........	147		142		151		140		580		
Mean per cent....		24.94		24.56		26.07		24.43			

standard deviations of the measurements are given in table 3 and may be compared with the observed values given in the last column.

The figures show that the observed standard deviations were greater in each case than the theoretical. This means that there is some agency operating to cause variability in height in excess of that to be expected on the basis of pure chance. The influences affecting the height of the plants were naturally greater in the case of the quartiles where the difference between the theoretical and observed values was greatest, namely in quartiles I and IV. This may be taken to mean that there is something in the genetical nature of the plants which was more potent in determining their height than the accident of location, and that this influence appears to be most effective on plants in the extreme classes.

Some additional light on the problem is afforded by the study of Harris (1921) in which he determined certain interperiodic correlations of the size of the *Helianthus* plants discussed above. When the measurements are thrown together into quintiles or quartiles, small differences between two individuals are likely to be given as much significance as large ones, provided they are large enough to throw the two individuals into different groups. While it is true that one must make classes in forming a correlation table, there are usually more classes and each individual has a better chance to count for what it really is.

The coefficients expressing the correlations between the size of plants either at antecedent or subsequent stages decreased as the periods became more widely separated in time. The coefficients were positive and constitute evidence that the size of the plant throughout the growth period bears a relation to its size when first measured. When the increments in height at different stages were studied, the coefficients of correlation were not so unanimous in their meaning, since some were positive and some were negative and many were statistically insignificant. However it appears that the increments of successive periods were generally positive and fairly highly correlated when the periods showed actual growth increments. When the periods were separated by any considerable length of time the coefficients were generally insignificant in magnitude and either positive or negative in sign.

The results of the two methods of investigation are essentially concordant in showing that plants which fall initially into the class of "small" or "large"

TABLE 4

Growth and variability of apricot trees measured as cross section of trunk

YEAR	AGE FROM PLANTING	MEAN	STANDARD DEVIATION	COEFFICIENT OF VARIABILITY
		sq.cm.		
1917	1	2.86 ± 0.31	2.09 ± 0.22	73.22 ± 11.24
1918	2	16.51 ± 0.88	5.84 ± 0.62	35.37 ± 4.22
1919	3	55.75 ± 1.68	11.17 ± 1.19	20.03 ± 2.22
1920	4	92.4 ± 2.12	14.04 ± 1.49	15.19 ± 1.65
1921	5	147.0 ± 4.07	27.0 ± 2.88	18.4 ± 2.02
1922	6	193.7 ± 5.4	36.0 ± 3.9	18.6 ± 2.1
1923	7	208.5 ± 6.22	41.2 ± 4.4	19.8 ± 2.19
1924	8	251.8 ± 7.66	50.7 ± 5.42	20.1 ± 2.24
1925	9	282.0 ± 8.47	56.12 ± 6.00	19.90 ± 2.21

individuals, though variable, tend to stay in that class throughout life.

Few students have given attention to the size growth of trees over a period of years, though many have reported on the fruit production. Data have been secured at this institution upon the growth and variability of a population of apricot trees. The area of the cross section of the trunk at a distance of 15–20 cm. above the bud union is used as the index of tree size and has been found to be reliable for this purpose. Each winter the circumferences of the trunks were measured and the area of the cross section calculated therefrom.

Table 4 shows the increase in size of a population of 20 unpruned trees, from the year following that in which they were planted in the orchard. The growth appears to follow the path of a logarithmic curve with the exception of the size in 1923. This lag may be due to the unusually heavy crop of fruit which these trees produced in the summer of 1922. The variability in this population was very high at the outset, but declined in three years to a level which it has since followed rather closely.

For the purpose of the present discussion it is somewhat more important to enquire about the relative size of these trees in successive years after the manner of the investigation of maize and sunflowers.

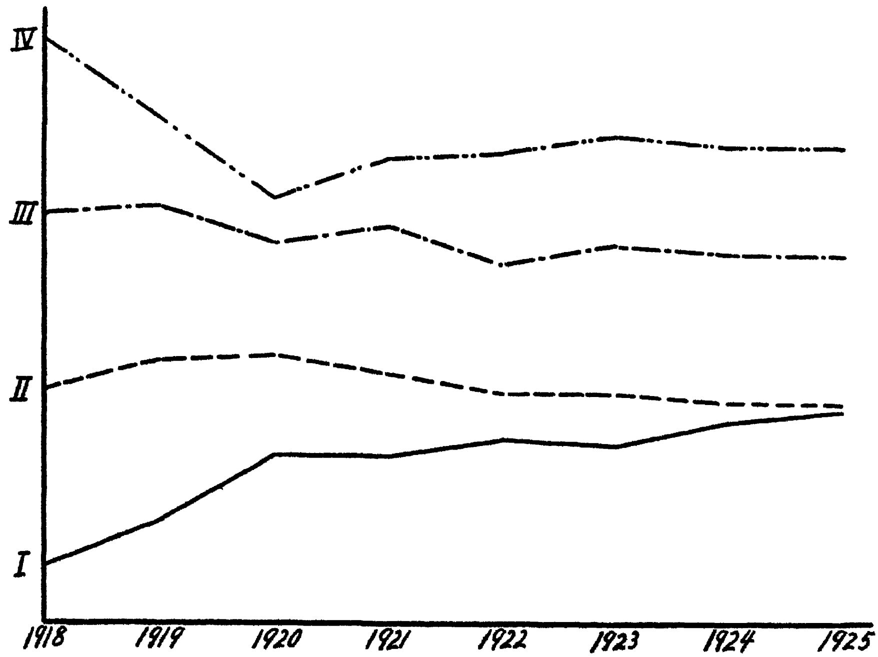

Fig. 1. Graphs Showing Changes in Mean Quartile Position in Succeeding Years of Apricot Trees Starting in the Various Quartiles

The size measurements of the 76 unpruned trees in the orchard were accordingly arranged in quartiles for each year and their distribution studied. The graphs in figure 1 show the distribution of the tree measurements in four quartiles of 19 trees each in 1918 and the mean quartile position of the same trees for the seven following years.

The average measurements of trees

whose size gave them a position in quartile I in 1918 were found in the group of smallest trees up to and including 1925, although some of them rose into higher quartiles. Quartiles II and III, the intermediate sized trees, showed relatively small fluctuations from their original values. Quartile IV, which was composed of the largest trees in 1918 retained that characteristic until the end, although the average quartile position of the trees was less than 3.5 most of the time.

Permanent size differences may arise from soil differences and from other environmental conditions, both of which may affect trees more profoundly than the shorter lived annual plants.

I shall not attempt a critical discussion of the genetical aspects of the inheritance of size, leaving it to those whose achievements in the field of genetics gives them authority to speak on it. So far as I can judge from their work, however, there is good evidence to support the assumption that size factors in an open fertilized population may be regarded as Mendelian characters which are distributed at random in the population.

2. *Age and variability*

The variability of leaves, shoots and fruits forms a means for judging of the action of inherent factors in the plant and may be regarded as an important phase of the subject of differentiation. Whatever views one may hold on the nature of hereditary factors, he is interested in the development of the organism produced.

The results of measurements of different characters are not so concordant as to express any pronounced relationship between age and variability in plants. Too many times the measurements have been made on some rather unimportant character and the plant as an entity has been disregarded.

The size of plants, annual or perennial, is generally more variable when young, though I found (Reed and Holland, 1919) that the variability in height of sunflower plants was a minimum at the end of the first week, increased during the next three weeks, and subsequently was fairly constant in variability. The coefficient of variation of maize (Pearl and Surface, 1915) and of apricot trees (table 4) was largest in the young plants and decreased with age. The number of veins in beech leaves (Pearson and Radford, 1904) was more variable in the first formed leaves on a spray than on those subsequently formed. The variability of the early nepionic leaves on *Sium cicutaefolium* decreased in successive leaves (Shull, 1905).

Records of the yields of fruits in consecutive years, while scanty, afford a larger basis for comparison. Orange trees (Batchelor and Reed, 1918) and apple trees (Hedrick, 1911) showed no more variability in yield over a period of six or seven years than for any particular year in the period. The probable errors of yields of black currants (Hatton, 1925) showed a great drop from the first year of bearing to the second, but no significant changes thereafter.

3. *The relation between the size of a shoot and that of the organ from which it grew*

It is believed that there is a relationship between the size of a vegetative organ and that of the stem on which it developed, but the problem is one which has not been quantitatively studied with the thoroughness which its importance seems to require. If we regard any particular organ as a parasite on its mother shoot, its size would depend to a large extent upon the supply and rate of

transfer of necessary materials to the young organ. If, however, we regard the relationship as one of commensalism, then it is clear that the only way in which one can determine the relations is by investigation of actual cases.

In the case of larger plants there is a difficulty confronting the investigator at the outset due to the fact that a stem produces a varying number of branches and that their size depends to a large extent upon their age as well as upon other factors.

The production of primary laterals on branches of the apricot tree does not indicate a high degree of relationship between the length of the branch and the total number of laterals it bore in the first year (Reed, 1924). If we adopt the following designations we may state the results in the form of coefficients of correlation:

a = number of laterals per branch
b = total length of laterals per branch
c = length of branch

The following coefficients of correlation were found,

$$r_{ac} = 0.337 \pm 0.067$$

and

$$_{ac}r_{b} = -0.313 \pm 0.013$$

which means that, if all the laterals were the same length, there would be a negative association between the length of branch and number of laterals produced.

The relation between the length of the branch and the length of the laterals it produced is, however, more to the point and we may note the correspondence between the two characters:

$$r_{bc} = 0.700 \pm 0.040$$

Since the number of laterals on branches was itself a variable it is better to take the coefficient of partial correlation which expresses the correlation in case each branch had the same number of laterals

$$_{bc}r_{a} = 0.665 \pm 0.042$$

The comparatively large value of this coefficient shows that the longer branches of the apricot tree tended very definitely to have longer laterals.

The problem of organ size in bean plants has been carefully studied by Sinnott (1921) with respect to the dry weight of leaf, pod, and seed. A part of the determinations were made on immature plants, but the majority of the measurements were upon plants at maturity. From his paper a few data may be quoted:

Dry weight of shoot : Average dry weight of leaf, $r = 0.769 \pm 0.015$
Number of leaves: Average dry weight of leaf, $r = 0.607 \pm 0.023$
Dry weight of shoot: Average dry weight of pod, $r = 0.301 \pm 0.033$
Total weight of fruit : Average dry weight of pod, $r = 0.460 \pm 0.029$
Dry weight of shoot : Average dry weight of seed, $r = 0.229 \pm 0.035$
Total weight of fruit : Average dry weight of seed, $r = 0.390 \pm 0.031$

The coefficients represent what might be regarded as a significant degree of correlation but upon more careful consideration of the original data one can hardly draw that conclusion. Sinnott skillfully showed that there is an increase in organ size with increasing body size up to a certain point only, and that beyond this point an increase in the size of the plant is not accompanied by an increase in the size of the leaf, pod or seed. His explanation of this relation is derived from the fact that the size of an organ is dependent, not on the size of the stem from which it arose but upon the size of the growing point; on this assumption the small plants are those which did not attain at maturity sufficient size to have

arrived at the maximum stem (growing point) diameter. In such plants a significant correlation might be expected. In the case of the larger plants, however, Sinnott suggests that there is no relation between body size and growing point size and consequently no correlation between body size and organ size.

The next problem was to investigate this possibility. It is of course difficult to measure the size of the growing point and the cross-sectional area of the stem is obviously unsuited for the purpose. Sinnott believes however that the cross-sectional area of the pith of the internode below the attachment of the organ is satisfactory for the purpose. He accordingly made measurements of leaf and pith area on twigs of *Acer saccharum*. The coefficient of correlation between the two characters was 0.807 ± 0.024 and the regression was linear, confirming the idea that the size of the plant organ is dependent, not upon the body size of the plant on which it is borne, but upon the size of the growing point from which it developed.

4. *The correlation between size of an organ and its position on the stem*

The shapes of plants which ultimately depend on the size and position of their parts are more or less characteristic. Casual observation is sufficient to distinguish a fir from an elm even at some little distance. Yet when it comes to a precise description of the arrangement of plant organs we seem to have little real quantitative information on the subject. A few decades ago the subject of phyllotaxis was quite extensively studied by those having leisure for such things, but we cannot see where their results contribute anything to the static or dynamic problems of growth as there was no concrete relationship obtained between size and position of leaf. It seems, however, that a study of the problem ought to be facilitated by an assumption that the pattern of the organism is the result of a process of growth and differentiation which is largely an expression of inherent factors.

We come to see a larger meaning in the words of Dutrochet (1822) "La tige d'un végétal quelconque, considérée dans son ensemble et abstraction faite des bourgeons adventifs, offriroit un aspect parfaitement régulier, si tous les bourgeons se développoient, si toutes les branches auxquelles ils donnent naissance prenoient un accroissement semblable ou proportionelle. Mais l'avortement d'un grande nombre de ces bourgeons, la différence de la nutrition, qui est active dans quelques branches et languissante dans quelques autres, amènent dans la tige du végétal une irrégularité qui n'étoit point originaire."

The functional relationships between the size of an organ and its position on the stem has received comparatively little study by botanists and even they have devoted attention to the seed-bearing rather than to the vegetative organs. The size of a leaf whorl (number of leaves) in *Ceratophyllum* was shown (Pearl, 1907) to increase in number from the proximal to the distal part of the plant in a way which was well expressed by the equation

$$y = A + C \log (x - \alpha)$$

"That is, the absolute size of the elements of the developing system given by a *Ceratophyllum* branch is modified by environmental differences, but the law which describes the proportionate differentiation of the elements is independent of the environmental history of the plant." This may be interpreted to mean that the size of any particular whorl of leaves is a

function (in the mathematical sense) of the number of whorls which have previously been formed on that axis. Pearl's work showed that the size of whorls on primary and secondary lateral branches also followed the same law of growth as those on the main stem.

Another relationship of importance was that of the variability in leaf-number of successive whorls. An extensive study of the coefficients of variability of leaf-number showed that the number of leaves on successive whorls were characterized by an ever increasing constancy to their type.

When the *Ceratophyllum* branches were studied with respect to their distribution on the stem, relations quite similar to the above were discovered. While the production of branches on the lower part of the stem was somewhat irregular so far as their location at nodes was concerned, their production became more regular as they approached the distal end of the stem.

The mean length of laterals on pear branches showed some tendency to fall on a curve of the form $y = a + bx - c \log x$ when y equals length of lateral and x represents the ordinal position of the lateral on the branch (Reed, 1921b).

The relations between position and length of fruiting branches of sea-island cotton (Mason, 1922) suggest a paraboloid curve but the author did not attempt to obtain an equation for it. This plant should yield profitable data for study because a fruiting branch is ultimately formed from the extra-axillary buds of every node of the central axis.

The problem of the distribution and the length of apricot shoots on the stem axis was briefly studied by the writer (Reed, 1924a). Casual observation of an apricot branch shows that primary laterals occurred in three fairly well defined groups. The laterals occupying the center of a group were those of maximum length, from which their length gradually decreased. The group of laterals nearest the proximal end of the branch was the largest and produced the longest laterals. The second group consisted of fewer and shorter laterals than the first, and was separated from it by an average of 20 nodes which remained dormant. The third group of laterals was not so well defined as the others, but showed many of the same features.

The symmetrical arrangement of the laterals in each group is a feature which suggested that their lengths conformed to a logarithmic curve.

When the scale of mean lateral length for each branch was arranged so that the center of group I fell on node 48, the three symmetrically shaped groups of laterals were easily distinguishable.

If we assume that the cyclic growth of the laterals was in some way similar to the cyclic growth of the branches which bore them, the summations of their length, beginning at the base of the branch should give a curve resembling that of growth. It was actually found that their values agreed closely with an equation of the general form

$$\log \frac{y}{a - y} = K(x - x_1)$$

where y = length of lateral grown from node x; x_1 = the node at which y had attained half the length of a for the cycle; a = the maximum, or limiting, value of y; and K = a constant.

If the lengths of the individual laterals be regarded as increments in the length of a system, then the differential form of the above equation ought to express their lengths for each nodal position.

$$Z = \frac{dy}{dx} = ky(a - y)$$

here $$k = K/A$$

This was found actually to be the case and the calculated values were in good agreement with the observed. The three curves showed the decreasing amplitude characteristic of the groups of laterals on the main branch.

A brief discussion of the relation between rate of growth and structure has recently been given by Penrose (1925). When each new part arising on a straight axis possesses growth properties similar in certain respects to those possessed by the apical group of cells, repeating structures are formed, e.g. fronds of the Male Fern or leaves of Fool's Parsley. In these instances the ability of the part to repeat the structure of the whole is expressed in three stages, the last being incomplete. More commonly the repetition in shape is limited to one stage, because the parts are not themselves similar in shape to the whole, but only to one another, though the size of the part bears a constant ratio to that of the whole plant. The dimensions of successive members form, in such a case, a geometrical progression, provided the system of growth is uniform.

Penrose gives examples to show that the sizes of successive leaves and of their internodes give values which closely approximate the curve of autocatalysis. The equation to the curve of outline of the plant structure is

$$x = A(1 - e^{-L/A})$$

Here x = the length of vein, leaflet, or internode; L = length of axis; A = the limiting or maximum value of x; and e = base of the natural logarithms. Obviously, this is the equation to a logarithmic curve.

The gradient in the growth capacity of homologous parts along an axis must be recognized. The leaves on certain parts of a stem are always smaller than those on the middle region. His data constitute further evidence of the usefulness of the autocatalytic curve in studying growth.

5. The length and frequency distribution of laterals on the branch in relation to the problem of growth and differentiation

In water one finds many plants showing a symmetrical development, indeed it is the best medium for the growth of simply organized plants. But the plants which live in a fluctuating environment are not usually symmetrical except in a very restricted way. It is possible that the universal tendency for development meets opposition of a kind that acts to bring about differentiation in an environment which is often sub-optimal.

There is recent evidence that the accumulation of metabolic products has a marked influence on growth and differentiation. The place at which they accumulate and the rate of transformation, may therefore play a part in differentiation.

The total output of differentiated material as measured by the length of lateral branches on a shoot tends toward uniformity (Reed, 1921b, 1924a). There is variability, of course, but no more than one finds in the lengths of the mother shoots themselves. The total lengths of laterals of pear shoots in the first year showed a root-mean-square deviation of less than 10 per cent of the mean. The resulting branch-patterns range from a system composed of few but long laterals to one composed of many, but short, laterals.

We may consider the length of the laterals on a branch, since this phase of differentiation is one which influences the pattern of the plant. The longest laterals are not necessarily the oldest, nor those at the extremity of the mother shoot.

The branches of fruit trees produce many more short laterals than long. When

histograms representing the distribution of length are drawn, they show an unsymmetrical distribution about the mean due to the higher frequencies in the lower classes. The distribution of short laterals on many trees determines in large measure their capacity for producing fruit. The distribution of apricot laterals has a pronounced asymmetry due to the predominance of short laterals. The mean length of 2528 primary laterals had a coefficient of variability of 110.53 ± 1.95. Asymmetrical distributions were also found in *Ceratophyllum* (Pearl, 1907), short branches being produced with much greater frequency than long branches.

These facts taken together are good evidence that the length of shoots on a tree or plant is governed by some very definite factor so fixed in its action that the law of chance is practically eliminated.

The number of blossoms per branch has been but little studied with respect to distribution, yet it is an important subject in differentiation. The blossom is a highly energized center on the vegetative organs toward which some of the most important synthetic materials migrate from other parts of the tree. The formation of a sufficient number of viable fruit buds is one of the obvious factors of success in the struggle for existence on the part of a species.

A survey of young apricot branches at the end of their first season's growth showed that the frequency distribution was asymmetrical owing to the more frequent occurrence of few blossoms per branch. The coefficient of variability of the mean was 60.39 ± 4.28.

Most of the blossoms were borne on the primary and secondary laterals of the apricot branch and there is naturally a relationship between fewer blossoms and shorter laterals, both of which have been shown to predominate on this tree. The ratio of blossoms on primary and secondary laterals of group I (the oldest group) was approximately 3:2, therefore the age factor does not seem to be the determinant for blossom-bud formation. The coefficient of correlation between the number of blossoms per branch and the ratio of primary laterals to total number of nodes per branch was

$$r = 0.386 \pm 0.065$$

The coefficient is positive and indicates that factors which cause the formation of numerous laterals also tend to form a larger number of flower buds. Of course the situation is more complex than this sounds, for example, the increased amount of photosynthates produced due to an increase in primary laterals would probably increase the formation of flower buds. Again it is possible that the formation of the two kinds of units (laterals and flower buds) is an expression of the same tendency to differentiation on the part of the tree.

Another step in the study of the problem consists in attempting to learn what relation there is between the length of a lateral and the number of blossoms it can produce. There is an opinion current that short laterals bear a proportionally larger number of blossoms, but the impression may be due to the fact that the blossoms on them must of necessity be closer together and hence more conspicuous.

In the paper cited (Reed, 1924a) the coefficients of correlation were determined with interesting results. If

a' = number of blossoms on primary laterals
b' = number of nodes on primary laterals
c' = length of primary laterals

the coefficients of gross correlation are

$$r_{a'b'} = 0.089 \pm 0.020$$
$$r_{a'c'} = 0.077 \pm 0.020$$
$$r_{b'c'} = 0.969 \pm 0.014$$

and the coefficient of partial correlation is

$${}_{a'b'}r_{c'} = 0.059 \pm 0.021$$

This coefficient shows plainly that there is no correlation between the number of blossoms and the number of nodes on a lateral.

Similarly for secondary laterals

$$r_{a''b''} = 0.118 \pm 0.018$$
$$r_{a''c''} = 0.122 \pm 0.018$$
$$r_{b''c''} = 0.971 \pm 0.001$$

and

$${}_{a''b''}r_{c''} = -0.002 \pm 0.018$$

Here there is no correlation between the numbers of blossoms and nodes upon the secondary laterals.

The frequency surfaces showing the association between nodes and blossoms brought out some important relations. They showed that in each case there were two rather well defined groups of laterals, (a) a large number of fruiting laterals and (b) a smaller number of distinctively vegetative laterals on which relatively few blossoms were produced. They also showed the essentially asymmetrical types of distribution in the two cases.

The relation between the position of a lateral and the number of blossoms it bore was also investigated, in order to see whether the lower (proximal) laterals produced more or less blossoms than the upper (distal) laterals on the branch. The coefficient of correlation in this case was

$$r = -0.109 \pm 0.022$$

This small degree of negative correlation may be interpreted to mean that the lower laterals were only slightly, if at all, superior to the others in the production of blossoms. These results indicate that the laterals of the apricot tree tend toward remarkable uniformity in the production of blossom buds.

Mason (1922) has briefly discussed this tendency for sea-island cotton plants to produce increasingly uniform numbers of nodes on fruiting branches. The coefficients of correlation were all positive and their values were greater for apical than for basal zones of the fruiting branches. "This was considered to indicate the presence of some factor which tended to limit the development of all fruiting branches, and that its influence became more marked as development proceeded." The removal of vegetative branches had a tendency to decrease the coefficients of correlation and suggested the introduction of an additional factor which definitely inhibited the development of the fruiting branches in the unpruned plants. Mason presented a hypothesis that this is due to the deflection of growth-promoting substances from the central axis system as a result of the unrestricted growth of the vegetative branches, and that the senescence of the central axis system is likewise ascribable to the deflection of these substances to the basal fruiting branches.

The effect of position upon the size of seed has been little studied. Harris (1915) found, however, some correlations between position and size of bean seeds which show a small, though positive correlation. This would mean that the weight of a seed is greater as the distance from the base of the pod increases. He has also shown (Harris, 1917) the existence of a negative relationship between bilateral asymmetry and the capacity of beans for maturing their ovules into seeds, that is, asymmetrical pods were less capable of seed development than symmetrical pods.

6. Age and size of vein islets

There have been investigations which produced evidence that the size of vein "islets" tends to decrease with age of the individual. The problem is rather difficult because of the inherent variability of the material and other investigators have come to the conclusion that there is no difference in the size of the so-called islets. We must therefore conclude that the question is still open.

7. Age and teratology

The proportion of teratological fruits in *Passiflora* was found (Harris and Gortner, 1914) to be a maximum among those first formed and to decrease as the plants became older.

On *a priori* grounds it might be expected that the tendency to produce abnormalities had some relation to the age of the individual, whether this consisted in the "wild oats" type of abnormalities due to the vigor of a young plant, or in the doddering imperfections of the senile period. The question is one of enormous importance in the evolution of a type or species, yet I find but few studies on it. It is a subject in which there is need of rigorous definition and exactness to avoid needless, not to say trivial, work.

IV. DIFFERENTIATION AND DEVELOPMENT

There is at present a hiatus in our ideas of the causal relationships between form and physiological forces, due perhaps to the fact that the chemical physiologist is less accurate in his analytical studies of the plastic shoot-forming substances than the biometrician who measures the products of the growth process. There must be a series of causal factors which bring about the more or less constant results in the form of individuals of this or that species of organisms. It will not suffice merely to weigh, measure, and correlate the organism unless we are content with a very limited view of the growth process. Most forms of life (except the most primitive) are characterized by an axial structure. Organisms living in a comparatively constant *milieu* have a relatively symmetrical structure. In a fluctuating *milieu* the untoward conditions are met by differentiation which leads to the production of an organism which lives on and produces offspring under conditions which would otherwise be prohibitive. The present state of our knowledge leads us to believe that much of the energy expended by the plant during growth goes to maintain an equilibrium between the organism and its environment which is favorable to the processes of development. A part of this energy may well be expended on differentiation.

1. The problem of dominance of the apical meristem

The axial structure which characterizes the higher forms of life results from a more rapid rate of growth in one direction than in others. The simple manner of growth of the filamentous thallophytes gives way to the many angled development due to localized meristems of root apices and of apical buds seen in the spermatophytes. The dominance of these meristematic regions impresses the casual observer, and since it is one of the most fundamental aspects of differentiation in plants we shall discuss recent studies on its action. Many of the statements found in the discussion of the question of apical dominance are vague and others are mystifying. The statement that "the available food materials of the stem are principally devoted to the development of the apical bud" raises more questions than it answers. The statement that the

growth on an upright branch is regulated by "polarity" falls into the same category. In the sense that polarity has been applied to the formation of shoots and roots upon cuttings, this idea would be inapplicable to the factors determining shoot or flower formation, since, in its implication, polarity involves the idea of two mutually exclusive qualities—for example, the opposite ends of a magnetized bar of iron. The idea of an "axial gradient" is a more exact designation of the phenomenon but does not account for the production of the gradient.

In recent years there has been a vital interest in this problem and we may discuss some of the investigations which have dealt with it.

Loeb (1916) explained the results of his experiments with *Bryophyllum* in the sense of Sach's theory of the upward flow of shoot-forming substances and the downward flow of root-forming substances which determine when and where dormant buds shall begin to grow. In his later work he advanced the idea of an inhibiting substance which was supposed to arise in the apical region and to move toward the subapical buds, keeping them in a dormant condition, while the apical buds were thereby freed from this substance and capable of growth. Subsequently he renounced this idea and believed that the inhibiting action of one part of the plant upon another is due to the fact that the sap begins to flow to the *anlagen* which first begin to grow, and that the other parts remain dormant because of the continuous flow of sap to the most active *anlagen*.

This idea of the effect of the flow of foodstuffs in producing polarity is seen in the writings of others. Curtis (1920) who is one of its most successful advocates has succeeded in destroying apical dominance in cuttings by injecting them with solutions of sucrose and other substances.

No more perspicacious views have been advanced than those of Robertson (1923) in ascribing the growth reaction in regenerating organisms to an autocatalyst which is produced in the cell nucleus and escapes into the pericellular fluid during mitosis. Cell division is regulated by the relative volumes of nucleus and cytoplasm (the nuclear-cytoplasmic ratio). Every cell then contains endogenous autocatalyst in the nucleus and exogenous autocatalyst in the pericellular fluid. Under conditions of equilibrium the sum of the amounts of endogenous and exogenous autocatalysts is a constant; if the endogenous supply is large then the exogenous supply is small, and vice versa. Hence if the supply of exogenous catalyst is large only a small supply of endogenous autocatalyst can be produced before equilibrium is imposed upon the reaction. Thus the substance produced by any part which is capable of influencing regeneration in any other part, is one which inhibits the growth of the part in which it is produced.

"The nuclear autocatalyst therefore combines in itself all the properties necessary to bring about the effects observed by Loeb, and we have furthermore merely to assume the existence of varying degrees of differentiation in the cells composing the fragment of stem to understand how one and the same substance, namely, the nuclear autocatalyst, may inhibit the multiplication of one type of cell while actually promoting the multiplication of another" (p. 211).

Studies on the process of growth in cuttings and in amputated shoots at this laboratory have yielded no little information upon the problem of uni-directional growth, or polarity.

Unusually strong dominance exists in

the apical regions of shoots of the pear tree (Reed and Halma, 1919). So long as the apical bud of a shoot grows uninterruptedly there is seldom any development of lateral shoots. If, from any cause, the apical bud of a shoot is arrested in its development, a neighboring lateral bud promptly develops and the shoot from it continues the axial growth.

If the apical portion of a shoot be amputated at the end of the growing season, as in the process of "heading back," several lateral shoots arise from buds directly back of the point of amputation and the most distal bud not only is the first to grow but also invariably produces the largest growth.

The lateral shoots which develop in such a case are progressively smaller as their distance from the apex increases. In a case already mentioned their lengths were expressed by the equation

$$y = 93.47 + 4.193\,x - 136.907 \log x$$

where y = length of lateral shoot and x represents its ordinal position (counted from the apex) on the parent shoot. These facts lead one to conclude that growth is influenced by some factor which is unequally distributed in the shoot.

2. *Factors controlling dominance*

This dominance of the apical region of the stems of Chinese lemon is so pronounced and characteristic that one can only conclude that it is due to some significant internal factor. Experiments were planned for the purpose of getting information upon the nature of the agent which instigated this apical dominance.

When cuttings of Chinese lemon shoots are suspended vertically in a moist atmosphere, shoots develop from buds at the apex of the cuttings and roots (usually from the callus) at the basal end. This occurs whether the cuttings are in the normal or inverted position. The cuttings will live and continue to grow for several months, but shoots develop only from two or three buds nearest the apical end of the cutting. If these buds are killed by burning them with hot glass rods, or gouged out, the buds next below them will develop, but if the apical buds remain functional and develop, the lower buds remain dormant. If the sprout from an apical bud be removed after having reached a length of a few centimeters, a new sprout will develop from one of the accessory buds but the lower buds remain dormant as before. If the tip of a sprout be removed, growth will continue from one of the lateral buds of the sprout, but the sub-apical lateral buds on the cutting remain dormant. Young shoots on the trees remain in an unbranched condition unless the tips are cut off.

The course of events may be followed somewhat more accurately when the growth of buds is inhibited by encasing them with material which mechanically prevents growth and which may be removed at any time. In our first experiments we encased the upper part of cuttings in a thick cast of plaster of Paris which prevented the development of the buds it covered. A few weeks later sprouts appeared from buds situated just below the plaster cast, as though they were apical buds. After the sprouts on each cutting in the experiment had reached a length of several centimeters, the plaster casts were removed and the cuttings suspended again in the moist chamber. In a very short time the buds at the apices of the cuttings began to grow out and sprouts were formed in the typical manner. As they grew the sprouts produced near the middle while the cutting was enclosed in plaster of Paris ceased growing and eventually some of them died, but the sprouts from the apical buds grew normally.

The quantitative relations of the effect of this sort of treatment have been studied in detail by Halma (1926) using Chinese lemon cuttings which were tightly wrapped with strong rubberized tape. Each cutting possessed ten buds. In one lot of cuttings the three distal buds were wrapped, in the second lot the five distal buds were wrapped, and in the third lot none were wrapped. The length of sprouts on each cutting was measured every few days. At intervals the tape was removed and record was made not only of the length of sprouts at that time, but of both subapical and apical sprouts at the end of the experiment. Growth started from buds on the unwrapped part of these cuttings only a few days later than from the apical buds of the unwrapped cuttings. After removing the wrappings none of the subapical sprouts died.

The growth of sprouts on both the wrapped and unwrapped portions of the cuttings follows the course of an S-shaped curve, suggesting the possibility that the two portions, although connected morphologically yet behave as separate physiological units. Upon further measurements of growth and variability of the material Halma concluded that they were physiologically distinct units. The same tendency toward apical dominance was manifested by each portion of the cutting. In 30 per cent of the cuttings whose upper three buds were wrapped the third bud remained dormant after the tape was removed. In the case of cuttings whose five uppermost buds were wrapped only 6 per cent produced sprouts from all five buds after the tape was unwrapped. As a rule only the first, second, and third buds developed, where five buds had been wrapped.

Halma cogently discusses the bearing of these facts upon the nature of regeneration in stems. "There is no doubt that the growth of the cuttings under the conditions of the experiment depends upon the material stored in the stem, and that this supply becomes exhausted regardless of the number or position of the sprouts produced. According to Loeb the sprout, or sprouts, which grow out first attract all the available material, hence the other buds remain dormant. The above investigation shows clearly that this is not true for Chinese lemon cuttings, because in many cases the sprouts below the inhibited portion were of considerable length before the tape was removed and yet growth was not prevented in the apical region.

The interpretation of the results of earlier experiments was based on the assumption that an inhibitory substance, produced by the growing apical sprouts, passed toward the basal part of the cutting and thus inhibited the development of sprouts in that region.

From this experiment, it is obvious that that assumption was inadequate, because in this case the apical region of the cuttings had no sprouts to produce an inhibitory substance and, furthermore, when apical sprouts were produced, these were unable to suppress the growth of subapical sprouts.

If we assume that dominance is due to an axial gradient of metabolism declining steadily with the distance from the apex, then a lemon shoot ought to produce a gradation of sprouts from apex to base. This gradation, however, appears only in a part of the shoot. Furthermore, less growth ought to be produced in the subapical than in the apical region. This was not the case with taped cuttings, where both the upper and lower portions produced growth in proportion to their mass. There is also no consistent difference in the amount of sprouts produced by the different parts of the mother shoots.

A possible explanation of these experiments is based upon the view held by

Curtis (1920) that some substance necessary for growth passes upward through the phloem. On this assumption, in the control cuttings the growth promoting substance would move upward until it reaches the uppermost bud or buds which are in condition to make use of it.

But cuttings planted upside down also produce sprouts from the apex, hence we cannot say that this substance can only move upward. We have seen that in the free portion of the taped cuttings sprout growth started later than in the apical portion of the control cuttings. This time factor is significant. We may assume that the transformation of food reserves into growth-promoting substances is a gradual process which begins at the apex. This view is strengthened by the fact that when only the three uppermost buds were inhibited, the delay in the outgrowth of buds immediately below the tape was not as great as when the five uppermost buds were inhibited.

No definite reason can be given as to why the transformation of food reserves into growth-promoting substances should begin at the apex. Evidently it takes place just as quickly in taped as in untaped cuttings for sprouts will break through weak places in the tape before there is any sign of growth below the tape.

The results obtained warrant the assumption that the earlier release from dormancy of the buds in the apical region is due to the gradual transformation of food reserves into growth-promoting substances from apex to base. The dormancy of sub-apical buds may be assumed to be due to the ability of the actively growing apical sprouts to draw on the entire supply of growth-promoting substances as fast as they are formed. If the growth of apical sprouts were dependent upon the supply of these substances which are present in that region only, then buds all along the cutting would have to grow out in order to account for the mass relation obtained.

It was also shown that the growing sprouts below the taped portion cannot draw on the supply of growth-promoting substances which are stored up in the apical part.

It seems to the writer that the above explanation is more plausible than that based on the downward flow of some inhibitor. A recent investigation by Gardner (1925) also indicates that nutritive factors are involved in the initiation of sprout growth."

Halma has discussed at some length the intraseasonal cycles of growth produced by lemon trees in their relation to the growth of sprouts. During the first period growth probably is produced at the expense of stored material, later it depends on materials manufactured contemporaneously. (Gardner (1925) has noted that starch disappears first from the apical part of a shoot as the spring growth begins and progressively disappears downward.) The transformation of food reserves into growth-promoting substances during the first period of growth in lemon trees begins probably at the apex and the supply is appropriated by the growing sprouts as fast as it is formed, hence the basal buds remain dormant. Since the subapical sprouts on the wrapped shoots were later in developing than apical sprouts on unwrapped shoots it seems reasonable to assume that the former can draw upon the supply of growth-promoting substance only when it lies below the point of origin of the sprout.

During the second period growth is confined to a few apical sprouts under favorable conditions. The amount of raw materials furnished each shoot depends upon the supply and the competition among different organs. We must seek an explanation for the fact that the upper-

most sprouts on a shoot grow so largely at the expense of those below them, i.e., for the continuance of polarity. No better explanation appears than that the rapidly growing apical sprouts exert an inhibiting influence upon the growth of those situated below them. This influence, as Loeb (1917) suggested, may be due to an actual substance (a chalone) which is produced in the growing tip and, passing toward the base, prevents further elongation of subapical sprouts. The inhibiting substance does not depress growth in the apical sprouts because ordinarily it is carried away as fast as it is formed.

These assumptions are well sustained by the results of numerous experiments which Halma performed on horizontal cuttings and shoots. When cuttings or unbranched shoots are placed horizontally, sprout development is confined to the dorsal side of the shoot except for one or two sprouts which develop on the ventral side near the apex of the shoot.

The results of several experiments go to show that this asymmetrical type of growth is due to the distribution of some growth-controlling factor and not to inherent differences in the constitution of the shoot. If all buds on the dorsal side were destroyed none of the buds on the ventral side developed into sprouts though adventitious buds on the dorsal side produced sprouts. For three consecutive years all sprouts on the dorsal side of horizontal shoots were rubbed off as fast as they developed yet none of the buds on the ventral side, with the exception of one or two near the apex, showed any sign of growth. When a horizontal cutting is allowed to develop sprouts from the dorsal side and is then rotated through an arc of 180 degrees, the buds from the previously ventral side then produce sprouts, while the original sprouts gradually cease growth and, in some cases,

When buds on the ventral side of a horizontal shoot were given a certain degree of isolation 73 per cent developed sprouts. The isolation was given by making a slanting cut, beginning about one centimeter on the distal side of the bud and extending into the wood to a point one centimeter on the proximal side of the bud. This severed the bud from the mother shoot except on the proximal side. A small plate of mica was inserted in the cleft to prevent the wound from healing. If the cut were made in the opposite direction, leaving the bud area attached on the distal side, none of the buds produced sprouts.

Quantitative studies on the growth of sprouts on horizontal shoots led to some satisfactory conclusions, and throw some light on the rôle of shoot forming substances in the formation of sprout growth. A lot of unbranched lemon shoots were bent and tied in a horizontal position before growth started in the spring. Half of the shoots were kept in this position during the entire season and the others were bent in the opposite direction when their sprouts had an average length of 5.4 cm. In less than two weeks the buds which were previously on the ventral side began to develop sprouts and although the growth of those now on the lower side was not suppressed, the growth of those on the dorsal side exceeded the others by a few centimeters in length when growth ceased for the season.

The evidence from the behavior of horizontal shoots goes to support many of the foregoing ideas of the factors which influence growth and differentiation. It appears that growing sprouts on the dorsal side are able to draw on the supply of growth-promoting substances which are contained in the dorsal as well as the ventral side of the shoot. Therefore, the growth on horizontal shoots was approximately equiva-

shoots which produced two sets of laterals. The longitudinal movement of growth promoting substances is slight because a notch below a bud on the ventral side prevents growth-promoting substances from reaching it, while a notch on the distal side permits it to grow but affects only that one bud. After the stored food reserves are utilized, notching on the distal side of buds on the ventral side is not effective in starting sprout growth from them. Therefore the initial period of sprout growth is evidently dependent on this accumulation of starch and other reserve material. We can hardly assume that the production of an inhibiting substance by the sprouts on the dorsal side prevents buds on the ventral side from developing because when all dorsal sprouts were rubbed off for three years no growth came from buds on the ventral side of the shoots. Furthermore, when sprout-bearing shoots were reflexed, a new set of sprouts grew from buds which had previously been ventral and the new set of sprouts showed no retarding effect on the original sprout until the end of the first growth cycle.

The appearance of sprouts on shoots which have been bent into a horizontal position is not to be explained easily. The result has been ascribed by some to the compression of tissues and consequent impediment to the flow of sap to buds on the ventral side of the shoot. The incorrectness of this view has been shown by experiments (Halma, 1926) with young lemon trees grown in pots. Their shoots were bent at right angles to the axis of the plant and tied in that position. One plant was inverted so that the compressed tissues were on the dorsal side and the other remaining in the normal position suffered compression on the ventral side. In both cases growth occurred only on the dorsal side of the shoot.

When sprouts appear on the first few nodes back of (basad to) the bend the evidence is more in favor of the view that there is an obstruction to the passage of nutrient substance (Gardner, 1925), because in one case they may be on the vertical and in another on the horizontal part of the shoot.

The idea of an obstruction to the upward flow of growth-promoting substances has also been used in attempting to explain the development of buds in cases where notches or girdles have been cut just above them. There are many obstacles to the acceptance of this idea, however. It is more probable that *physiological activity* and not *accumulation* is the condition which initiates growth. The apical part of a cutting is normally the most active region physiologically, but it is possible by artificial means to raise the physiological activity of another region to such an extent as to make it dominant so far as shoot production is concerned. Jones (1925) found that a difference of no more than 2°C. was amply sufficient to convert a warmed into a dominant region, irrespective of its position in relation to the apical end of the cutting. When whole cuttings of seakale (*Crambe maritima*) roots were thus treated shoots could be induced to arise from the root-apex end if a higher temperature was maintained at this end of the cutting. "It seems legitimate to conclude from these experiments that whilst the whole of the cambium has potentiality for bud production, this gains expression chiefly in regions where the cambium is exposed and physiologically most active."

3. *The metabolic gradient*

There is yet to discuss the theory of the "metabolic gradient" which has been formulated by Child (1915). Although it adds little to our understanding of the causes which determine differentiation in the plant, it is an admirable statement of

the problem and gives us a convenient framework upon which to arrange our ideas. It emphasizes the kinetic aspect of the problem by relating the differentiating processes to increased or decreased metabolic activity. The problem of differentiation is not so much a question of the presence of organs as of their position and relative size. It seems to me that the solution of this problem must in large measure depend upon activity and less on the Sachsian concept of shoot- or root-forming substances. Child considers that the intensity of metabolism, measured by intensity of respiration or response to stimuli, shows a definite variation in different parts of the organism, indeed in a single organ, and that these gradients determine the fundamental outlines of axial symmetry and structural differentiation. Centers of high metabolic activity like the head of a planarian worm or the apex of a stem tend to dominate centers of lower metabolic activity. Gradients may be reversed or obliterated, or new gradients established by environmental conditions which modify the metabolic rate in different parts of the organism, but the gradient once established, persists through asexual and perhaps through sexual reproduction.

It is difficult to conceive that every possible activity of the organism is dependent upon a gradient of substances appropriate thereto. One soon has the plant full to overflowing. But to consider that the gradients may represent gradual changes in the nuclear cytoplasmic ratio governing the activity of the autocatalyst may clarify our ideas on the subject.

V. CONCLUDING DISCUSSION

The foregoing subjects have been discussed with the hope of clarifying our understanding of the problem of growth and differentiation in plants. If this incomplete treatment has any merit it consists in directing the attention to recent work on the problem, and to the importance of quantitative studies in this field.

Growth is a complex process, yet it is surprising that the application of a few simple mathematical operations should throw so much light upon its nature. If the discussion has erred on the side of over-simplification, it is because it seemed best to lay aside all irrelevant matters and discuss growth as a slow transformation of material at a rate proportional to time. This ought to emphasize the fact that the forms and functions of organisms, though variable, nevertheless are not outside the realm of exact science. Much additional work is needed to discover the quantitative relationships governing the so-called pattern of organisms. It seems reasonable to expect that the position as well as the size of organs bears a definite correlation with certain properties (morphological or physiological) of the other parts of the organism. The examples discussed here and elsewhere, justify the expectation that an extension of quantitative work will do much to obtain that orderly, verifiable mass of knowledge which can truly be termed *science*.

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DIFFERENTIAL FERTILITY

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THE PROBLEM

THERE has been a great dearth of adequate data from which to determine the relative degree to which the different social and economic classes of any human population reproduce themselves. This is particularly true for the population of the United States. At the same time the problem is clearly one of first class importance both theoretically and practically. It is the reproductive activity of the persons now living which determines the constitution of the population of the next generation to an overwhelming degree. Especially is this true in any country where there is naturally, or by legislative restriction, a limited immigration.

The pioneer attempt at an adequate statistical approach to the problem of differential fertility amongst the several social classes in a human population was that of Heron (1906). Using the correlational calculus he reached the following conclusions:

> As far as the present investigation goes it demonstrates I think conclusively that for the London districts there is a very close relationship between undesirable social status and a high birth-rate. In districts where there is overcrowding, where there is a superabundance of the lowest type of labour, where it is needful to employ many young children in order to earn daily bread for the family, where infantile mortality is greatest, there the wives of reproductive ages have most children. Where there is more culture and education as shewn by a higher proportion of professional men, where there is more leisure and comfort as shown by a higher percentage of domestic servants, where the traders who appeal to the improvident and thriftless are fewer in number, there the birth-rate is least. Again, where there is more general pauperism, where signs of bad environment like phthisis are prevalent, where pauper lunatics are most plentiful, there the birth-rate is highest. Cancer alone of the undesirable physical conditions dealt with so far seems more prevalent in the prosperous and cultured districts and to be associated with a lower birth-rate.
>
> Nor is the higher birth-rate of the undesirable elements compensated by the higher death-rate. The net fertility of the lower status remains higher than that of the superior status.
>
> The relationship between inferior status and high birth-rate has practically doubled during the last fifty years, and it is clear that in London at least the reduction in the size of families has begun at the wrong end of the social scale and is increasing in the wrong way. I have brought forward evidence enough to shew that the birth-rate of the abler and more capable stocks is decreasing relatively to the mentally and physically feebler stocks.

Broadly speaking these conclusions have been confirmed by all subsequent students of the problem, and have become incorporated into the accepted body of present sociological doctrine. I shall make no attempt at an exhaustive list of the literature. The following citations sufficiently support the point, and will lead the inquiring reader into the further literature: Brown, Greenwood, and Wood, 1920; Cattell, 1915–17; Cobb, 1912; Crum, 1914; Darwin, 1922; Elderton *et al.*, 1913; Fürst and Lenz, 1926; Gini, 1926; Hart, 1924; Hewes, 1911; Hill, 1913; Holmes and Doud, 1918; Johnson and Stutzmann, 1915; Lenz, 1926; Marshall, 1913; Near-

ing, 1914; Onslow, 1913; Pearson, 1909, 1910; Popenoe, 1917; Phillips, 1926; Savorgnan, 1923; Schiller, 1926; Spiegelberg, 1924; Sprague, 1915; Terman, 1925; Weinberg, 1909; Whetham, 1909.

Holmes (1921) sums the case up in the following words (p. 140):

> The elements of the population that are of subnormal mentality exhibit at present the highest degree of fecundity. This is the general verdict of most students of the birth-rate of different classes of the population. The higher death-rate of the subnormals probably does not offset completely their greater fecundity. . . . The classes in the higher social strata . . . . in general have a birth rate which cannot fail to lead to extinction. This much is clearly indicated from a variety of sources, while the springs of our defective inheritance have shown no manifest signs of drying up.

There have appeared in recent years a considerable number of studies on the fertility of groups of college and university graduates. The results have been generally held to be alarming in greater or less degree. Such socially desirable folk are not reproducing at anything like the rate desired by the conscientious eugenist.

But college graduates almost certainly do not include quite all the socially desirable people in the world. What is needed before a final alarmed judgment is reached is a fairly representative cross-section of all the different sorts of people composing the population. Brown, Greenwood, and Wood (1920) end their careful and enlightening study with these words (p. 205):

> The sociological implications of these results are left for the discussion of others. Here the personal impression is recorded that the analysis of the sample of middle class families has led to no result incompatible with the conclusions drawn by Professor Karl Pearson and his collaborators from wider data of a different kind.
>
> Whether these results, or any results of wider analysis, suggesting that neglect of eugenic principia is leading to a steady deterioration of the race are likely to influence the reproductive habits of the educated classes or social legislation designed to modify those habits, is a question we need not attempt to answer.

Reading between these lines, and also reading their first conclusion (p. 205): "In the first place, it is plain that there is no essential difference between the fertilities of women who have and of women who have not received a university education. Such differences of effective fertility as appear can be fully explained by differences of age at marriage," there arises some conviction that these English authors would be in sympathetic agreement with the second sentence of the preceding paragraph.

SOME NEW DATA

In the last issued report on natality from the United States Census Bureau (Birth Statistics, 1923) there is a table (numbered 10, pp. 171–181) which makes available some new and welcome data regarding differential fertility in this country. Once more the student of human biology is deeply indebted to the wisdom and insight of Dr. William H. Davis, who so ably and intelligently directs the collection and tabulation of the vital statistics of the United States. It is my purpose now to discuss briefly certain aspects of this new material. A preliminary report of this study, in which I was aided by Dr. John Rice Miner, has been published elsewhere (Pearl, 1926).

The data apply to the United States birth registration area *exclusive* of Delaware, Maine, Massachusetts, New Hampshire, Rhode Island, and Indiana. That is, the figures include California, Connecticut, Illinois, Kansas, Kentucky, Maryland, Michigan, Minnesota, Mississippi, Montana, Nebraska, New Jersey, New York, North Carolina, Ohio, Oregon, Pennsylvania, South Carolina, Utah, Ver-

mont, Virginia, Washington, Wisconsin, and Wyoming.

The original table provides the following information: The births, number of children born, and living, and average number born and living, to mothers of 1923, by occupation and age of father. The occupations of the fathers are grouped into the following main classes, with a number of smaller sub-divisions in each main class:

1. Agriculture, forestry, and animal husbandry.
2. Extraction of minerals.
3. Manufacturing and mechanical industries.
4. Transportation.
5. Trade.
6. Public service (not elsewhere classified).
7. Professional service.
8. Domestic and personal service.
9. Clerical occupations.

When one considers carefully the subdivisions under these nine main heads the usual difficulty with official vital statistics is at once encountered. Economically and socially differentiated groups are included in some particular general class from the remainder of which they are, in these respects, sharply set apart, in reality. But it is reasonably obvious that economic and social factors and forces are among the most important elements in determining the biologically significant environment of human beings, as they exist here and now. Relative wealth virtually determines the character of the immediate physical environment in which men live. Furthermore, economic and social position are significantly correlated with the amount of physical labor which individuals perform, and this has been shown (Pearl, 1924) to be biologically important.

In view of these considerations it was deemed necessary to reconstitute the main occupational classes, as given in the original document cited, so that they might conform at least somewhat more closely to significant reality. The general plan followed in this reconstitution of the classes was to take out of classes 2, 3, 4, 5, and 6, all subgroups in which the persons composing the subgroup enjoyed a distinctly and obviously higher economic and social position than the average of the main class as a whole from which they were removed, and put them into a reconstituted class 7. This procedure involved the following transfers: Operators, officials, and managers from Class 2, Extraction of minerals; builders and building contractors, and managers, superintendents, manufacturers, and officials from Class 3, Manufacturing and mechanical industries; captains, masters, mates, and pilots, and officials and superintendents (steam and street railroads) from Class 4, Transportation; bankers, brokers, and money lenders, commercial travelers, insurance agents and officials, and real estate agents and officials from Class 5, Trade; and officials and inspectors (city and county), and officials and inspectors (state and United States) from Class 6, Public service.

These transferred sub-divisions were then all put with Class 7, Professional service, as originally constituted. This latter class, as reconstituted, then includes not only professional men in the strict sense but the capitalists, officials, and managers, whose economic and social status is more like that of the professions than the other classes, so far as it was possible to treat them separately. In some cases this was not possible, as in the class Retail and wholesale dealers. Importers and exporters, and many of the retail dealers would be of the same economic and social class as the occupations which have been included with Professional service, but a majority of the class are probably small shop-keepers, and it

was therefore thought best to leave them under Trade, on the ground that probably a smaller error would be involved in so doing than in adopting the alternative procedure.

The net upshot of this manipulation is to leave all the main occupational classes except 7 composed chiefly of laborers, more or less skilled, but still persons whose living depends upon the daily performance of more or less routine tasks, *in contrast to* the persons composing the reconstituted class 7, who, in the large, get their living rather more by the exercise of their wits than of their muscles.

In order that there may be no misunderstanding the names of the main occupation classes which have been altered by the above described procedure will be printed in *italic* type throughout the remainder of this paper. This typographical usage will serve to indicate that the statistics so printed are for the *reconstituted* classes, and not for the classes originally so named in the official report.

The next and final point of method to be considered before coming to the results is that of age. The desideration in all studies of fertility is, of course, the completed family. In the present case, as usual, this desideration cannot be precisely attained from the available data. General consideration of the problem, and careful examination of all the figures themselves as given in the original report, led finally to the decision to deal analytically with the data for fathers aged 45 and over. This procedure will probably give as close an approximation as it is possible to get, from these or similar records extracted from the official standard birth certificate of the United States, to the unknown average size of completed family for the different occupational classes. In the textual portion of the original report from which the data are taken is the following statement (p. 20): "Particular attention is called to the data for fathers aged 40 to 49 years as these on the whole probably represent completed families." It is only after very careful consideration that I have ventured, in the treatment of the material here, to depart from the implication of the statement quoted. That 40 is too low a limit seems to be indicated by the figures themselves. In a majority of cases in the detailed tables the average number of children ever born is higher in the age group 45–49 than in the group 40–44. Again the detailed figures indicate that the inclusion of fathers over 50 in the group does not sensibly alter the averages which would be obtained by dealing with the age period 45–49 alone.

FERTILITY BY OCCUPATIONS

Table 1 presents the first set of basic data which we shall need in the discussion.

Before discussing at all the results of this table, it is necessary to consider some of the important peculiarities of the data. In the first place, if the figures of column (d) could be regarded as representing exclusively completed families, which they almost but not quite can, they would still give an erroneous impression of the gross fertility of the several occupational classes, for the following simple reason. All the data in the table are derived from the experience of women who were mothers in 1923. That is to say, they were women who were fertile in that particular year. No other women are included. No sterile matings appear, and no matings of generally low fertility throughout the mated life, except the few in which the female chanced to have a baby in 1923. That there are very few of such low fertility matings included is evident if it is recalled that we are here dealing only with families in which the father

was 45 years of age or over in 1923. In general the vast bulk of men who engender a baby when they are 45 years old, or over that age, are probably persons whose whole marital history has been characterized by relatively high fertility, as compared with the rest of their same social class.

The net result is that the values in columns (d) and (e) of table 1 somewhat exaggerate the true average fertility of the whole population of the same age in the various occupational classes. The probable magnitude of this exaggeration will be discussed farther on. The figures represent the average size of family of a selected sample only of the total population in each class, *the basis of the selection being high and probably historically continued fertility*. This means that, in the best case, we can only discuss from these data relative and not absolute fertility values. I see no reason to suppose that the relative fertility of the most fertile portions of the populations in the several main occupational classes, as given by these data, are not safely comparable. The only essential difficulty with the figures is that the universe of discourse which they encompass is a definitely limited one, and we cannot safely generalize beyond these bounds.

With these limitations in mind it is easily deduced that the mothers of children born in 1923 by fathers aged 45 years or over, on the basis of column (d) of table 1, had total average progenies up to and including the 1923 birth, which stood in relative positions according to the occupations of the fathers as shown in table 2. These relative sizes of average families are shown graphically in figure 1.

From these data it is seen, in the portion of the population here under discussion, that when the average size of family produced by a mother of 1923 in her total reproductive life up to that time, by a father who fell in the *Professional* class and was 45 years of age or over in 1923 is taken as 1.0, the average size of family

TABLE 1

Children born to mothers of 1923, by fathers aged 45 years or over, by occupation of father, in reconstituted general classes of occupations

OCCUPATION OF FATHER	TOTAL BIRTHS (a)	TOTAL NUMBER OF CHILDREN EVER BORN (b)	TOTAL NUMBER OF CHILDREN LIVING (c)	MEAN NUMBER OF CHILDREN EVER BORN (d)	MEAN NUMBER OF CHILDREN LIVING (e)	MEAN NUMBER OF CHILDREN DEAD (f)	PER CENT OF CHILDREN DEAD (g)
Agriculture, forestry and animal husbandry	41,825	289,140	251,833	6.91	6.02	0.89	12.9
Extraction of minerals	4,117	32,677	26,609	7.94	6.46	1.48	18.6
Manufacturing and mechanical industries	32,875	216,996	179,601	6.60	5.46	1.14	17.3
Transportation	4,480	27,002	22,997	6.03	5.13	0.90	14.9
Trade	6,771	34,885	30,389	5.15	4.49	0.66	12.8
Public service	949	5,189	4,374	5.47	4.61	0.86	15.7
Professional service	5,828	24,386	21,672	4.18	3.72	0.46	11.0
Domestic and personal service	2,424	12,820	10,799	5.29	4.46	0.83	15.7
Clerical occupations	1,677	7,149	6,296	4.26	3.75	0.51	12.0
Totals	100,946	650,244	554,570	6.44	5.49	0.95	14.8

produced from the mothers of 1923 by fathers who fell in the occupational class *Extraction of minerals*, and similarly aged 45 years or over in 1923 was 1.9. In general it appears that the relative average size of family in the different occupational classes in the case where we are dealing throughout with the selected more fertile moiety of the population, is in good general accord with what we have learned to expect from earlier studies in England and other countries. The professional, capitalistic group exhibits the lowest average size of family, and the labor groups, whether in factories, farms, or mines, the highest.

But from a racial viewpoint the matter

TABLE 2

Relative average size of family

Professional service	*1.00*
Clerical occupations	1.02
Trade	*1.23*
Domestic and personal service	1.27
Public service	*1.31*
Transportation	*1.44*
Manufacturing and mechanical industries	*1.58*
Agriculture, forestry, and animal husbandry	1.65
Extraction of minerals	*1.90*

needs to be pushed farther. There are a great many more farmers, or factory laborers, for example, in the whole population of the Registration Area than there are professional men. Let us next examine this aspect of the matter with some care. Table 3 lists the main occupational classes (reconstituted) in the same order as does table 2. In table 3, column (a) gives the number of males in each class who were 45 years of age and over at the time of the census of 1920. These are reduced in column (b) to relative figures, taking the reconstituted *Professional service* class as 1.00. Column (c), headed "Number of more fertile families in group, 1923," is a repetition of column (a) of table 1. This, it will be recalled, gives the number of births to mothers of 1923 in that year, by fathers who were 45 years of age or over. As has already been pointed out, those families within each

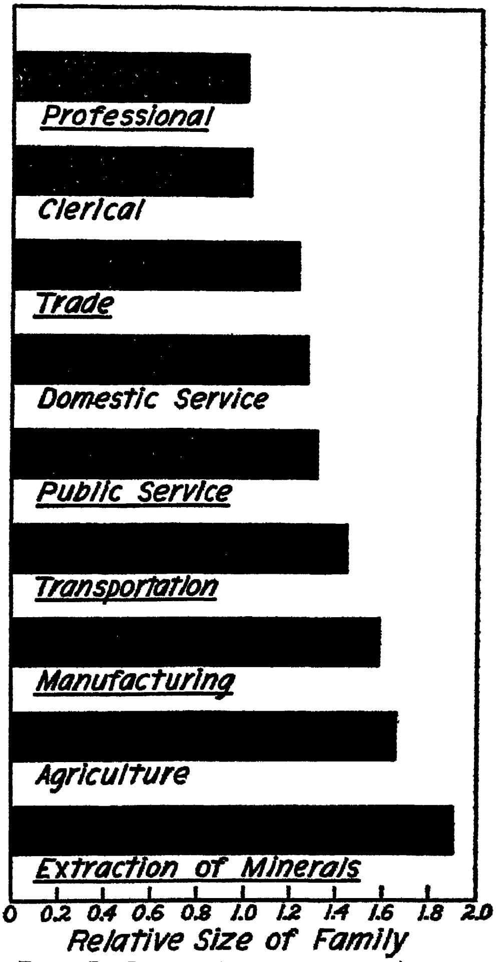

FIG. 1. BAR DIAGRAM SHOWING RELATIVE AVERAGE SIZE OF FAMILY EXPERIENCED BY MOTHERS OF 1923 IN THEIR REPRODUCTIVE LIVES UP TO THAT DATE, ACCORDING TO OCCUPATION OF FATHERS WHO WERE, IN 1923, 45 YEARS OF AGE OR OVER

occupational class, in which the wife had a baby in 1923 and in which the husband was at the time 45 years of age or over, represent on the whole the more fertile families in the group, taking the whole reproductive life together. Except

for small corrections, which ought to be made for multiple births and perhaps for illegitimate births, the number of births to these mothers and fathers, as given in column (c), gives the number of such "more fertile" families in the group. Column (d) gives the relative values of the figures in column (c), the *Professional service* class being again taken as 1.00. Column (e) is a repetition of column (b) of table 1. It gives the total number of children ever born in the "more fertile" families recorded in column (c). Finally, column (f) gives the relative values of the data in column (e), the *Professional service* class being taken as 1.00.

TABLE 3

Absolute and relative figures for population and fertility

OCCUPATIONAL CLASS (RECONSTITUTED)	MALES AGED 45 AND OVER IN GROUP, 1920 (a)	RELATIVE PROPORTIONS OF ITEMS IN COLUMN (a) (b)	NUMBER OF MORE-FERTILE FAMILIES IN GROUP, 1923 (c)	RELATIVE PROPORTIONS OF ITEMS IN COLUMN (c) (d)	TOTAL NUMBER OF CHILDREN EVER BORN TO FAMILIES IN COLUMN (c) (e)	RELATIVE PROPORTIONS OF ITEMS IN COLUMN (e) (f)
Professional service	*624,180*	*1.00*	*5,828*	*1.00*	*24,386*	*1.00*
Clerical occupations	215,188	0 34	1,677	0.29	7,149	0.29
Trade	*626,321*	*1.00*	*6,771*	*1.16*	*34,885*	*1.43*
Domestic and personal service	296,480	0.47	2,424	0.42	12,820	0.52
Public service	*141,265*	*0.23*	*949*	*0.16*	*5,189*	*0.21*
Transportation	*480,095*	*0.79*	*4,480*	*0.77*	*27,002*	*1.11*
Manufacturing and mechanical industries	*2,011,722*	*3.22*	*32,875*	*5.64*	*216,996*	*8.90*
Agriculture, forestry, and animal husbandry	1,899,128	3.04	41,825	7.18	289,140	11.86
Extraction of minerals	*167,172*	*0.27*	*4,117*	*0.71*	*32,677*	*1.34*
Totals	6,461,551		100,946		650,244	

The relative figures of table 3, Columns (b), (d), and (f), are shown graphically in figure 2.

The results exhibited in table 3 and figure 2 are of a good deal of interest, and in some ways unexpected. Broadly what the figures show is that:

1. For each male 45 years or over in the class *Professional service* in 1920, there was 0.34 of a male of corresponding age in Clerical occupations; 1.00 in *Trade;* 0.47 in Domestic and personal service; 0.23 in *Public service;* and 0.79 in *Transportation.* In these six occupational classes more-fertile families, as defined above, occurred in about the same proportions relative to the *Professional service* class taken as 1.00 in both instances, as column (d) and the dash line of fig. 2 show. This means that in these six occupational groups more-fertile families are represented in about the same relative proportions to each other, as occupied males of corresponding age in the classes as a whole. This is only approximately true, because the figures of Column (a) are for 1920, and those for (c) for 1923. But the general consonance of the relative figures for the six classes named will probably not be significantly disturbed by this consideration.

2. For every male 45 or over engaged in *Professional service* in 1920, there were 3.22 workers of corresponding age in *Manu-*

facturing and mechanical industries; 3.04 in Agriculture; and 0.27 in *Extraction of minerals*. But for every more fertile family, as here defined, in the *Professional service* class, there were 5.64 such families in the *Manufacturing* class; 7.18 in the Agriculture class; and 0.71 in the *Extraction of minerals* class. What these results mean is that families of more than average in the more-fertile families is not widely different from the proportion, always relative to the *Professional* group as 1.00, in which the several occupations are represented in the general male population, so far as concerns the first six occupations in Table 3. This means that in these six occupations the total fertility up to 1923, in the more fertile group with

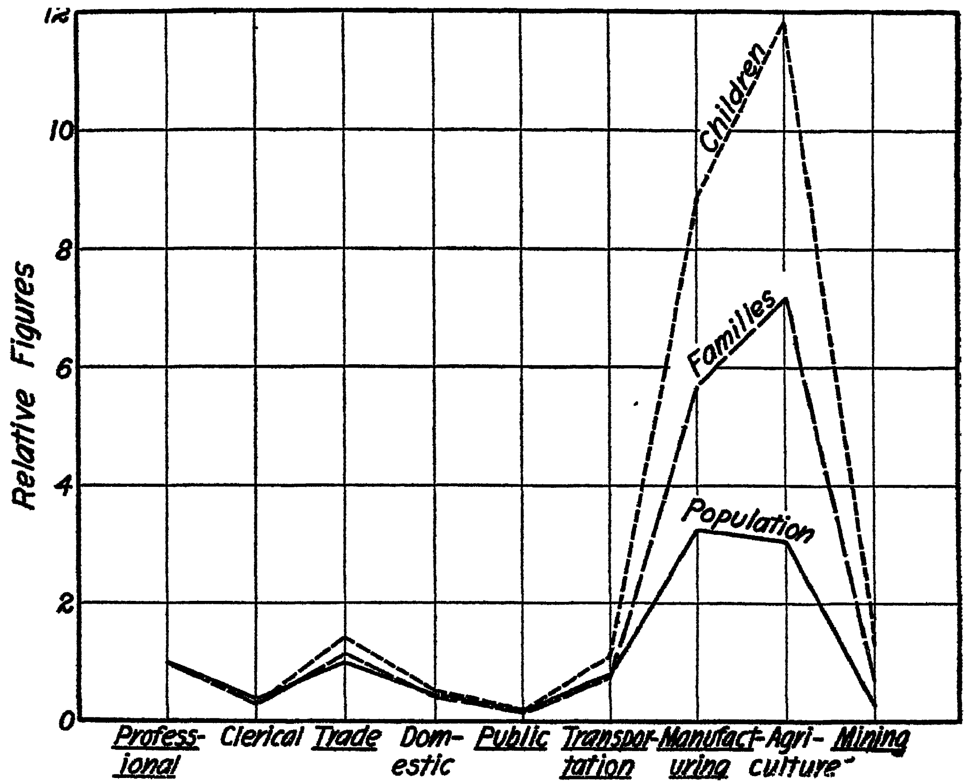

FIG. 2. RELATIVE POPULATION AND FERTILITY BY OCCUPATIONAL CLASSES
The solid line is the graph of column (b) of Table 3; the dash line of column (d); the dot line of column (f)

total fertility occurred in these three classes, in proportion to the male population of corresponding age, taking the *Professional* class as 1.00, from two to three times as often as they did in any of the six occupational classes discussed above.

3. The relative total number of children ever born, up to and including 1923, which we are dealing, was nearly in simple proportion to the size of the groups themselves, having regard to age, and when the *Professional service* group is taken as 1.00 in each instance. But in the three occupational classes *Manufacturing*, Agriculture, and *Mining* the case is quite different. Whereas there were 3.22 times as many males aged 45 and over in the

Manufacturing class in 1920 as in the *Professional* class, the females mated to males in the *Manufacturing* class had produced, up to and including 1923, 8.9 times as many children as had the females mated to the corresponding portion of the males in the *Professional* class, in the same period. In 1920 there were 3.04 times as many males 45 years of age and over in the Agriculture class as there were in the *Professional*. But the total production of children up to and including 1923, by the more fertile moieties in the classes, had been 11.86 times as great in the Agriculture class as it had been in the *Professional*. In the *Extraction of minerals* class there were only 0.27 as many males 45 years of age and over as there were in the *Professional* class. But the production of children up to 1923 had been 1.34 times as great in the former class as in the latter.

So far we have considered the populations, more-fertile families, and total children ever born, of the several occupational classes, only in relation to the *Professional* group taken as 1.00. This procedure gives a correct picture of the situation so far as strictly inter-class comparisons of the unit elements are concerned. But it does not permit entirely correct conclusions to be drawn in respect of the important question as to the proportionate contribution of each occupational group to the total population of the next generation. The proper base for the relative figures here is furnished by the *totals* of columns *a*, *c* and *e* of table 3, each taken as 100 per cent.

The results of treating the data in this way are shown in table 4 and fig. 3.

TABLE 4

Fertility of the occupational groups relative to the total population

OCCUPATIONAL CLASS (RECONSTITUTED)	PER CENT IN EACH CLASS IN 1920 OF MALES 45 AND OVER (a)	PER CENT OF MORE-FERTILE FAMILIES IN 1923 (b)	PER CENT OF TOTAL CHILDREN EVER BORN TO FAMILIES IN COLUMN (b) (c)
Professional service	*9.66*	*5.77*	*3.75*
Clerical occupations	3.33	1.66	1.10
Trade	*9.69*	*6.71*	*5.36*
Domestic and personal service	4.59	2.40	1.97
Public service	*2.19*	*0.94*	*0.80*
Transportation	*7.43*	*4.44*	*4.15*
Manufacturing and mechanical industries	*31.13*	*32.57*	*33.37*
Agriculture, forestry, and animal husbandry	29.39	41.43	44.47
Extraction of minerals	*2.59*	*4.08*	*5.03*
Totals	100.00	100.00	100.00

While the general trend of figure 3 is the same as that of figure 2, as it is in fact bound to be, figure 3 brings out an additional bit of information that is not shown by figure 2. What figure 3 shows is that in the first six occupational groups (*Professional*, Clerical, *Trade*, Domestic, *Public*, and *Transportation*) the more-fertile families in each group form a smaller percentage of the total number of more-fertile families than the males 45 years of age and over, in that same group, do of the total number of occupied males of the same ages. The single cross-hatched column is shorter, in every one

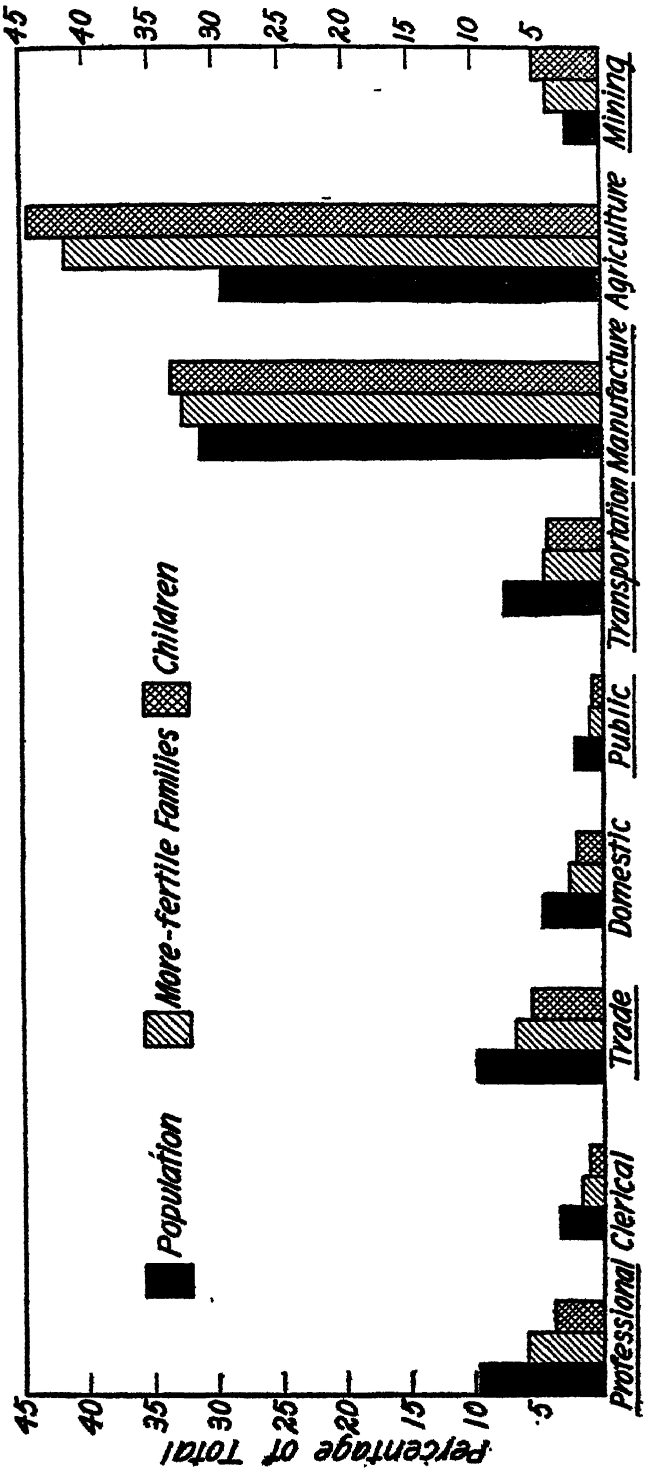

Fig. 3. Graph of the Three Percentage Columns of Table 4

of these first six occupational groups, than is the solid column. Similarly in these same six occupational groups the number of children ever born in each group forms a still smaller percentage of the total number of children, than either the males 45 years and over or the more-fertile families in each group do of their respective totals. The double cross-hatched columns in these six occupational classes are shorter than either the solid or the single cross-hatched columns. These results mean that the men aged 45 and over in these six occupational classes have not contributed to the next generation in as high a proportion as their own representation in this generation.

The case is diametrically opposite for the last three occupational groups (*Manufacturing*, Agriculture, and *Extraction of minerals*). In these three groups the percentage of children ever born, and the percentage of more-fertile families is *higher* than the percentage of males 45 years of age and over in the total population of occupied males. In each of these three occupational groups the double cross-hatched column is taller than the single cross-hatched column, which in turn is taller than the solid column. The men aged 45 and over in these three occupational classes have contributed to the next generation more than their own proportionate representation in this generation. The excess contribution is particularly marked in the case of the farmers. It is convincing statistical confirmation of the conclusions reached by Pearl (1925) regarding the sexual activity of farmers, from an entirely different sort of data.

SOCIAL AND EUGENIC IMPLICATIONS

Summing the whole case up it appears that the great laboring groups, *Manufacturing*, Agriculture, and *Mining*, not only have a higher proportion of more-fertile families per unit of population so occupied, than do the other occupational groups, but also they have a much larger average number of children per family. Put in another way the case comes to this: In our population it appears that the *Professional*, Clerical, *Trade*, Domestic and personal service, *Public service*, and *Transportation* occupational classes are reproducing themselves in such manner as not to maintain in quite its present status their relative representation in the population. But the heavy laboring classes, *Manufacturing*, Agriculture, and *Mining*, are reproducing themselves in excess of their representation in the population. From this excess must necessarily be supplied the deficiences in the first six classes in the next generation, if these classes are to maintain about the same representation in the total population that they exhibit in the present generation.

What is the racial, social, and economic significance of this result? It has generally been viewed with great alarm. The fact that college graduates, from whom are necessarily recruited most of the *Professional* class, are not proportionately reproducing themselves has been more than once represented as a sort of national calamity. The arguments that this situation is wholly deplorable are so familiar that I shall waste no time in detailing them. Instead I wish briefly to direct attention to another view of the case—one which I have never seen stated before with any clarity, and one which I believe deserving of careful consideration.

In a theoretically ideal social organization there would obviously be an optimum number of persons engaged in each of the numerous differentiated occupations, which when integrated together are essential to the well-being and survival of the society as a whole. There is

theoretically an optimum number of teachers, lawyers, store-keepers, laborers, soldiers, and so on. But in actual human societies there is no extraneous, god-like determination of these optimum relative numbers in the occupational classes. Instead the actual existing number is determined by a process of natural selection, in which process economic factors are probably the most important element.

But another factor comes also into the case. The human units wear out faster in some occupations than in others, and therefore need to be replaced faster. Roughly speaking the occupational classes are listed in table 3 in descending order of average duration of life. The only important exception is in the case of farmers. And in that case, while the total duration of life of farmers is, on the average, somewhat greater than that of persons in occupations higher up the list, it is not so if attention is paid solely to *duration of economically productive life*. The old farmer is generally a retired farmer, so far as actual work at farming is concerned.

One other consideration also needs attention. This is not only an industrial country, but a country in which the increase of prosperity and well being is almost solely dependent now, has been for some time in the past, and presumably will be for some time in the future, upon the continued *growth* of industry. This is shown clearly in figures 4 and 5. Figure 4 is taken from Pearl (1922), and figure 5 from Rylands (1926).

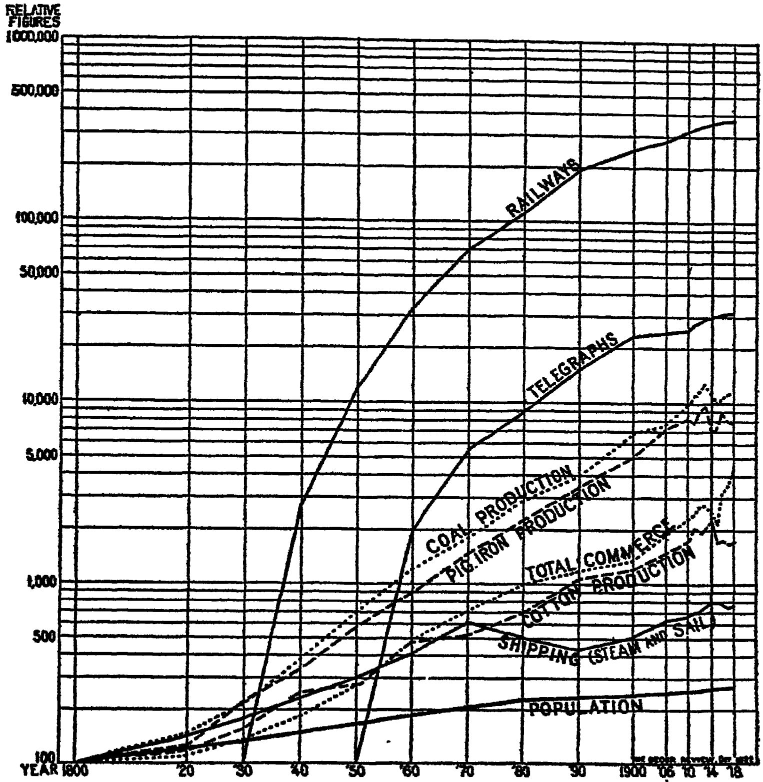

Fig. 4. The Progress of Population and of Industrial Production in the World, during the Nineteenth Century. (From Pearl, 1922)

What figure 4 demonstrates, I think, is

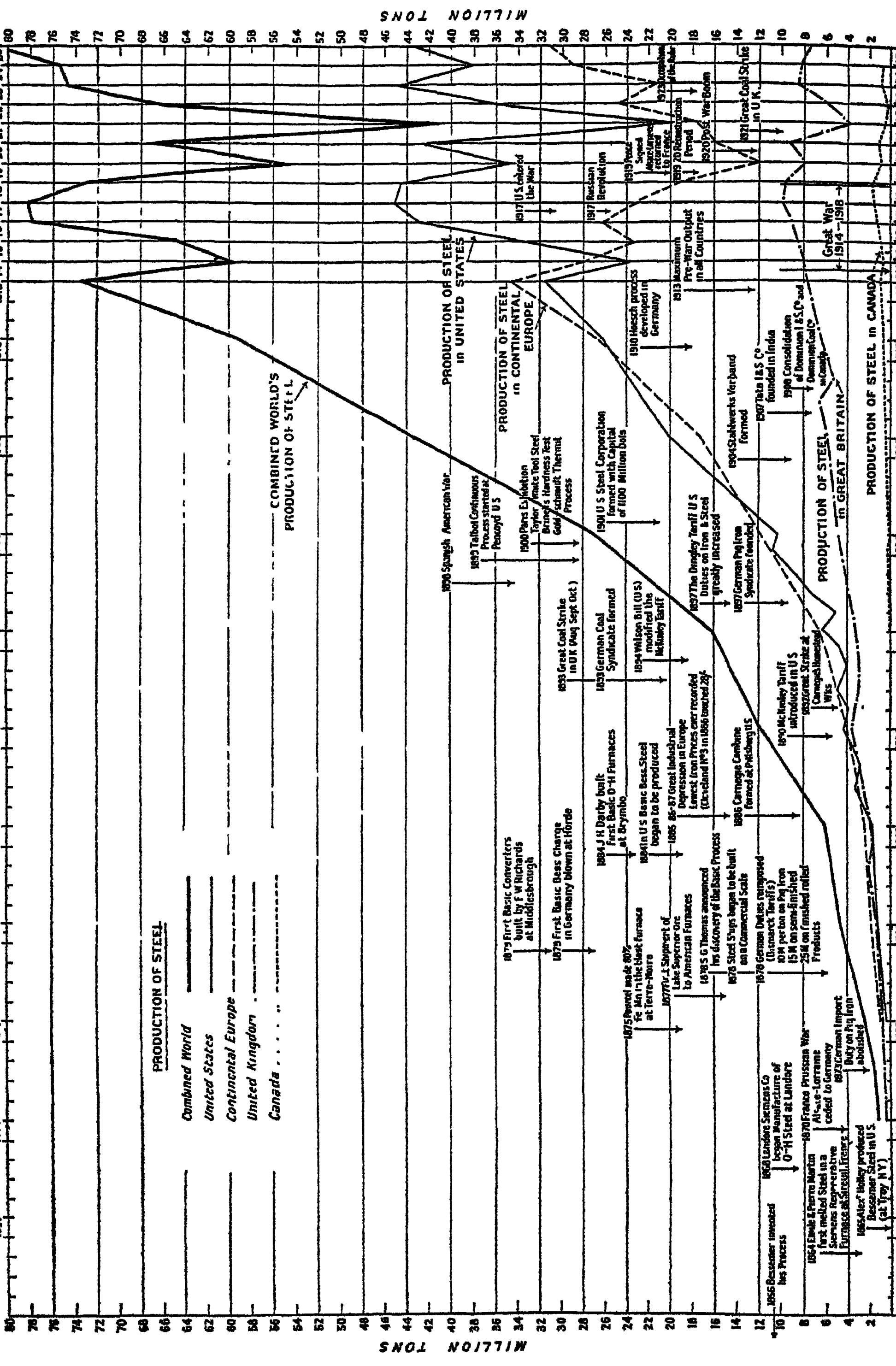

FIG. 5. THE WORLD PRODUCTION OF STEEL. (FROM RYLANDS, 1926. REPRODUCED, WITH THE AUTHOR'S PERMISSION, FROM PROOF COPY OF HIS PRESIDENTIAL ADDRESS)

that in order to permit the population to increase roughly two and a half times, and enjoy the standards of living which prevail at the present time, it has been necessary to increase coal and pig iron production from 50 to 70 times, the cotton production 20 times, the railway mileage 3000 fold, and so on. It is only because the organization of industrial processes, inventions, and scientific discoveries have made possible the growth of industry of all sorts at the rates indicated that human beings have been able to enjoy the standard of living that they have and do, and at the same time permit the population to grow as it has. Figure 5 in a slightly different way tells the same story.

The hard facts shown in figures 4 and 5 mean further that all along there has had to be an increasing production of laborers, skilled and unskilled, in the manufacturing and mechanical industries. Machinery alone does not make a profitable factory. There must be workmen to run the machines.

While figure 4 relates to world conditions figure 5 shows that so far as the most important and basic of the mechanical industries is concerned, the same conditions prevail to a striking degree in the United States, considered by itself.

Now, I suggest that the findings of this paper regarding fertility in this country are not widely divergent from what they theoretically ought to be if our society is to continue in general prosperity and well-being, and continue to grow in these respects. In short we *need* to have laborers reproduce faster than the first six occupations on our list, in order first to take up the greater human wastage in the laboring classes, and second to permit of continued industrial growth and prosperity. Probably a sound economic structure of the country as a whole is in a very real and considerable sense dependent upon just this relationship. So far from being alarmed at the present situation, I am disposed to think that we should find serious cause for *real* alarm if it were markedly different from what it is. Though the biological processes involved are widely different in the two cases, the actual facts about differential human fertility are curiously reminiscent of what obtains among the social insects. A stable and economically sound society there, as with us, seems to demand an excess production of workers.

The facts set forth in table 4 plainly mean that some part of the next generation's supply of professors, doctors, lawyers, bankers, railroad presidents, and the like, will have to be recruited among the sons of the farmers and factory laborers of this generation. But what of it? Just precisely this relationship has always been true so far in the history of the world and probably will be true for a long time to come. And furthermore from just the same sources will have to be recruited some of the clerks, typists, small tradesmen, job-holders, brakemen, motormen, and various other less lofty citizens.

In the United States the agricultural group has for a long time produced far more than enough children to maintain its own industry, as has been shown by McFall (1925). These farm boys in excess, so to speak, have contributed in no small measure to the highest intellectual, social, and economic classes of our population. In fact the agricultural class has demonstrated an especial fitness to contribute sound stock to other occupational classes. I am disposed to believe that time will show that the industrial class in our large cities is, in already measurable and probably increasing degree, doing the same thing. Let one observe the origin of the most brilliant and able students today

in city high schools, both classical and technical.

Wheeler (1926) has ably argued, and made a sound case, that the next emergent "level" above mind is the social. He says (p. 435):

> One of the levels in which the situation, as it appears to me, is most open to investigation, is the social. Unfortunately the subject has been passed over by writers on levels with only a few vague remarks. Unfortunately, also, the science of comparative sociology has remained undeveloped. It has, in fact, fallen between two stools, because the sociologists have left the study of animal and plant societies to the biologists and the latter have been much less interested in these societies as such than in the structure or individual activities of their members. Apart from Forel and myself only a few investigators, like Espinas, Waxweiler, Petrucci and Deegener, have evinced a keen interest in nonhuman societies. Yet these, no less than human society, are as superorganisms obviously true emergents, in which whole organisms function as the interacting determining parts. Owing, moreover, to the loose and primitive character of the integration and the size of the components even in the densest societies, it is possible to ascertain the behavior of the parts and to experiment with them more extensively than with chemical and organismal wholes, since the parts of the latter are either microscopic or ultramicroscopic and are always so compactly integrated that analysis becomes very difficult and involves a considerable amount of statistical inference.

What may be said, with any critical insight, to be statistically known about differential human fertility indicates that in these phenomena we have an expression of a very subtle but far-reaching and extremely significant mechanism of self-regulation in the social super-organism. The falling birth rate and death rate and the type of occupational differential fertility discussed in this paper are primarily to be regarded, I believe, as adaptive regulatory responses—that is, biological responses—to evolutional alterations in the environment in which human society lives. In this environment the economic element is perhaps the most significant biologically. This is not the place nor the occasion for the elaboration of this theme. But one cannot but be impressed that the almost total neglect by eugenists of the obviously important influence of relatively simple economic factors upon the human situation with which they deal, and which they endeavor to account for in very far-fetched and highly inferential ways, is stupid.

Finally regarding the specific results set forth in this paper, I frankly do not see the usually alleged cause for eugenic alarm, for the reason that history demonstrates, I believe, that the superior people of the world have always been recruited from the masses, intellectually speaking, in far greater numbers than they have been reproduced by the classes. And in saying this I do not for one moment subscribe to the view that environmental influences have been the chief factor in the production of superiority. On the contrary I adhere firmly to Galton's view that heredity plays the principal rôle. But the almost infinite manifoldness of germplasmic combinations can be relied on, I think, to produce in the future, as it has in the past, Shakespeares, Lincolns, and Pasteurs, from socially and economically humble origins.

In order that there may be no misunderstanding it should be emphasized that what has been said in this paper relates entirely and solely to the *relative* or *differential* aspect of fertility, as between the several occupational classes, and *not* to the absolute fertility of the population as a whole or its component parts. That the population of the United States as a whole cannot go on increasing at its present rate per unit of time, and its component elements continue to enjoy the standards of living which they have in the past and do now, would seem to be obvi-

ous. This conclusion has been many times emphasized in recent years, by various students of the population problem, particularly East (1923), and the present writer (Pearl, 1922, 1924, 1925), both of whom have expressed, and still adhere to the view, that birth control is a rational and intelligent method of counteracting the evils of excessive population growth. There is nothing in the results or conclusions of the present paper which in the least conflicts with this prior conclusion. That the absolute levels of birth rate will continue to fall in all social and economic classes, as it has in the past, with increasing density of population, seems highly probable. All that is here argued is that a differential birth rate—a higher rate of reproduction in some social and economic classes than in others—is probably to be regarded as a biologically normal feature of the social and economic structure of large human groups, and that this fact is not necessarily a sound ground for eugenic alarm.

Finally to assume that this paper states that the unlimited reproduction of genetically unsound stocks is not a dysgenic menace, is simply a confession that the paper has not been read. It would, of course, be highly desirable if the reproduction of all stocks exhibiting traits universally admitted to be undesirable and known to be inherited, could be completely stopped. But it has yet to be demonstrated that either poverty or lack of membership in a social aristocracy are biologically inherited traits, though the inference is too often drawn that they are. The present paper is intended, in part, to show that the eugenic condemnation of whole social or economic classes, either directly or inferentially by the contention that only certain classes such as college graduates are eugenically desirable, is unwarranted by anything now known. While this is not the place to go into the matter in detail I am convinced that the current orthodox position of eugenics rests upon a fundamental genetic fallacy which largely invalidates some of its most important conclusions. This matter I hope to discuss in detail in the near future.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will usually appear in each number one longer critical review of a book of particular significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

THE TENDENCY TO SOCIAL LIFE

Being a review of *Les Sociétés d'Insectes, leur Origine–leur Évolution*, by William Morton Wheeler. Paris (Gaston Doin), 1926. $4\frac{1}{2} \times 7$; xii + 469. 18 Fr.

By Philip P. Calvert, University of Pennsylvania

This volume belongs to the series *Encyclopédie Scientifique*, one of which (by L. Cuénot on *l'Adaptation*) was reviewed at length by Prof. J. H. Gerould in the QUARTERLY REVIEW OF BIOLOGY for January, 1926 (pp. 119–123).

Perhaps the first impression which one receives upon seeing the title of this new book by Prof. Wheeler is that it is a French version of his *Social Life Among the Insects* (New York, Harcourt Brace & Co.) of 1923. The latter volume comprised the author's Lowell Institute lectures of March, 1922; the new book contains his discourses as exchange professor from Harvard University to the University of Paris in 1924–25. Prof. Wheeler takes pains to correct such an erroneous idea in his opening pages, telling us that while he has made use in part of the material of his *Social Life*, in which he emphasized the fundamental rôle of nutrition in the development of the various insect societies, he here proposes to treat, in a more technical way, of these four questions:

1. What are the social insects?
2. Can it be shown that they have had an evolution?
3. If so what are the characteristics of this evolution and what methods should be employed to elucidate them?
4. To what general causes or conditions can we refer this evolution?

The advance in knowledge of the habits of insects in the three years intervening between the appearance of Prof. Wheeler's two books is shown by the fact that his list of distinct cases of social organization in this Class has increased from 24 in 1923 to 30 in 1926. The additions are the Bethylidae, Masaridinae and Trypoxyloninae among the Hymenoptera, the roaches (genus *Dasypoma*), the mole cricket (*Grylloptalpa*) and *Zorotypus*, a member of the recently discovered order Zoraptera. Twelve of the 30 groups listed in 1926 have definitely social members, the remaining 18 are believed to be in an imperfectly social (subsocial) condition. For these latter the existing data are too meager to make possible a satisfactory account of the development of

their social life. Here attention is given almost exclusively to the Aculeate Hymenoptera and the Termites. The rise and progress of social life in these groups are deduced from the fossils, now fairly numerous, morphological and taxonomic data and those of geographical distribution, together with comparisons of the habits of living insects.

The tendency to social life ("*tendance associative*" of Petrucci, 1906) is considered an appetition, like those of hunger and of sex, weaker but more continuous, less spasmodic and consequently less evident. Since all societies of insects are families, that is, affiliations between parents (usually a mother) and descendants, the attainment of the social condition is due to an increase in duration of her individual life and in her interest in her offspring. Pearl (1924) has suggested that the length of life of an animal is in inverse ratio to the activity of its metabolism. Prof. Wheeler thinks that the diminution of metabolic activity (which should, according to Pearl, prolong the life, especially of fertilized females) may be due to the fact that all the social and subsocial insects live in small cavities in soil or in wood, or in the interior of paper nests. Such abodes restrict or inhibit muscular movements. The living medium is dark, poor in oxygen, of uniform and rather low temperature. All these conditions tend to reduce metabolism and activity and to favor an accumulation of the fat in the body. The fecundity of the females is to a certain extent a function of their longevity as expressed clearly in the great size of the adult colonies of the higher termites, ants and the hive bee. On the other hand, the smallness of the completed colonies of various primitive ants and termites appears to be a consequence of the shorter life of the queen mother.

In his attempt to determine the phylogeny of the social Hymenoptera, Prof. Wheeler accepts the interpretation of Tillyard that certain recently discovered Permian fossils from Kansas represent a new order of insects, the Protohymenoptera, which by their wings (the only parts preserved) are intermediate between the Mecoptera (scorpion flies) and the Hymenoptera. The leaf-feeding sawflies of the families Pamphiliidae and Xyelidae (suborder Phytophaga) can be considered as the most ancient of living Hymenoptera. From such forms the entomophagous sawflies conduct us to the very archaic family of the Trigonalidae, referred by some to the Aculeate (stinging) Hymenoptera, by others to the Terebrantia (Parasitica); at the Trigonalidae these two series diverge from the ancient Phytophagous trunk. Near the base of the Aculeata the Bethylidae are to be placed and although this family is certainly very ancient and not to be regarded as ancestors of the social Hymenoptera, yet in the Scleroderma group of this family are realized conditions analogous to those in which the social habits of wasps, bees and ants originated. In this group the long-lived mother subsists on the same food as her young, is interested in them, licks them and can rear several broods successively. When the mother and her female descendants, or several females of different broods, are enclosed in the same receptacle with a larva of *Cyllene*, there is no rivalry between them, as one might expect, but on the contrary they coöperate to paralyze the prey and to lay their eggs on it in common.

Among the wasps, from *Synagris* to *Vespa*, the development of social life is characterized by the gradual appearance and differentiation of a caste of workers, by the increasing complication of the architecture of the nest, by the increase

in population of the colonies and by the larger size of the fertile female or queen. The annual development found in many members of this family fixes very definite limits to the extent of the population and retards or prevents all ulterior progress in social development.

The bees are the most numerous in species of all living Aculeates. They are imperfectly known and their taxonomy has yet to be worked out satisfactorily; different authorities have supposed them to be mono-, di-, or even tri-phyletic, although usually deriving them from the fossorial wasps (Sphecidae). In the development of their social habits, however, and in their nests they present an extraordinary parallelism to the Vespidae. The origin of wasp or bee communities from one or more than one female—monogyne or polygyne—is considered to be of minor importance depending on the mutual tolerance or animosity of the queens.

In seeking for the origin of ants, it appears to Prof. Wheeler that the group which merits the most serious attention is that of the Tiphiidae, and especially the genus *Elis* (*Myzine*). This family has affinities of structure and of habits with the Bethylidae, mentioned above. Six species of ants are known from the Eocene but they are not more primitive or more generalized than those of the amber and the latter are almost as highly specialized as those now living. These facts and the deeply rooted xerophilous tendencies of ants suggest their very probable origin in the Trias, if not at the end of the Permian, on great plains and interior continental plateaus, such as Australia presents today. Their first abode was on the surface of the soil, whence arose the subterranean, deserticolous and arboricolous habits, the last displayed by the most specialized genera of the whole family. Prof. Wheeler will not bring the ants across now submerged transatlantic or antarctic bridges from continent to continent and his inclination is toward a northern circumpolar centre of distribution for many of the genera.

The social bees although descended from the Sphecoids are, nevertheless, in many respects nearer to the social Vespoids than are the ants, descendants of (solitary) Vespoids. The explanation is no doubt to be sought in the evolution of the ants having been longer and more fertile in events.

Traits which the social Aculeates received from their solitary (non-social) ancestors comprise 1. A pronounced sexual dimorphism, 2. The storing of food for the young, 3. The construction of a nest, and 4. The defensive reactions of the female. As consequences of social life there have been added to these "solitary" bases a spermatheca which can preserve the sperm alive for so long a time that the fertilized female becomes potentially a hermaphrodite, capable of producing both sexes; a differentiation of the females into two castes, queens and workers, the latter again into workers properly so called and soldiers, while the male remains stationary and conservative; the mutual exchange of food between the members of the community (trophallaxis); the common utilization of collected stored food; the nest constructed by many instead of by one individual; and the defensive functions, more efficient and formidable than before, relegated to the workers or to the soldiers.

In the social aculeates the male has remained essentially in the condition of that sex as it existed in the solitary ancestors. He has not entered into the social activities; he is simply tolerated as indispensable for fertilization. The contrary is the case in the termites, where the various morphological specializations and the division of labor are shared equally by individuals of both sexes. From

the human point of view the termites thus appear as more perfectly social than the societies of aculeates and Prof. Wheeler asks whether, if, in some future metempsychosis, the choice were offered to one of us between the lot of an ant and that of a termite, the latter would be preferred!

Handlirsch (1903) placed the origin of the termites in the Cretaceous, but Prof. Wheeler thinks it may have been more remote. Fossil remains are not known from periods earlier than the Tertiary. Morphological data indicate their relationship to the roaches. As in the ants their present geographical distribution may be explained without recourse to intercontinental bridges.

The view here adopted as to the Mecopteroid origin of the Hymenoptera necessarily denies any genetic connection between the termites and the social aculeates. The fundamental differences between these two groups arise from the mode of formation of their respective colonies. In the former the colony is founded by a royal pair, in the latter by a fertilized female, either alone or accompanied by a swarm of workers. The termites, having preserved the ametabolic [the reviewer would prefer to say heterometabolic] type of ontogeny characteristic of the whole Orthopteroid series, have not realized the intimacy between the adults and the young which is correlated with the legless impotence of the immature aculeates. That the termites have not acquired the extraordinary instincts of the social aculeates is ascribed "sans doute" to their immediate ancestors not having traversed a stage of carnivorous and predatory habits and to their own life in great part in the midst of their food. The ultra-conservative habit of devouring wood and of living in the cavities thereof furnishes the key to comprehension of most of the social peculiarities of these insects. The cumbersome food and its slow digestion by the intestinal Protozoa have brought about the use of stomodaeal and proctodaeal foods with the resultant wide infection of the community with the flagellates and amoebae. Life in the interior of wood has led to degeneration or loss of the eyes, especially in the workers and soldiers, loss of pigment, often a thinning of the chitin, light-fleeing and water-seeking tendencies, and such means of defense as the cephalic glands of the soldiers and the building of solid nests.

While the descendants of an unfertilized hymenopterous female are generally males, there is no necessary connection between this fact and the polymorphism of the social insects. This is sufficiently proved by the termites in which both sexes arise from fertilized eggs and are equally polymorphic. In the Bethyloid Aculeates several genera have two forms of fertile females, one winged, the other wingless; here polymorphism precedes sterility. It is not improbable that the first ants may have preserved the dimorphism of the females after having become social. From such a beginning the reduction of the wingless females to workers may have occurred. This hypothesis may explain such observed conditions as the single apterous queen in the Doryline and other ants, the simultaneous presence of winged and wingless queens in the same colony (*Ponera*), or in different places (*Harpagoxenus*), the frequent existence of ergatomorphic queens (*Leptogenys*, *Onychomyrmex*), etc.

The polymorphism of the termites is not only more complicated in itself than that of the ants but it also affects both sexes equally. Soldiers are present in all termites, except in the genus *Anoplotermes* (where they disappeared second-

arily) while in the ants they are definitely developed in only a few genera. In termites the soldiers precede the workers phylogenetically. In ants the reverse is the case. In ants there is only one general type of soldier, the "mandibulate," which is also very general in termites, but is replaced in the higher members of this group by a second or "nasute" type. Ant soldiers differ less from the queen and workers of the same species, in the size and conformation of the head and mandibles, than is the case with termite soldiers and their respective workers and sexual forms.

The problem of polymorphism still preserves a "complexité exaspérante." At least six different interpretations of the origin of the castes can be formulated. Lack of data concerning the causes of blastogenic determinism render a discussion of some of these interpretations useless and attention is consequently directed here to the effects of different modes of feeding the larvae.

The slight differences between the workers and queens of social wasps and of bumble bees are susceptible of explanation by a quantitative difference in food. In the social bee *Trigona* the larger quantity of food supplied to the queen larva appears to hasten the development of ovaries, while the qualitative difference in the food of the two female castes of *Apis* appears to accelerate the maturing of the eggs in the queen and to reduce in her some parts which are better developed in the worker.

The great variety of nourishment supplied to the young of ants prevents the demonstration of a relation between food and the differentiation of the castes, but the first broods of single queens founding new colonies are always small workers. Later broods are workers of larger size and it is only after production of the largest workers that queens appear. This applies to other monogyne aculeates also and to termites. The soldier caste of ants corresponds rather to the workers of termites, phylogenetically if not functionally; it appears not to have been differentiated from that of the large workers before the middle of the Tertiary, to have arisen independently in most of the genera in which it is present and not to have acquired a definitive representation in the germ plasm.

If the views set forth in the early part of this book be accepted, Prof. Wheeler conceives that we might admit that the queens and workers of the Formicidae and the royal forms and soldiers in the Isoptera are really blastogenic, but that the other castes and especially the pleomorphic forms of workers and of soldiers are trophogenic. A very interesting discussion is given of considerations which bear on blastogenic versus trophogenic origins: 1. The extraordinary stability of the typical castes in the existing species of ants and of termites; 2. Their extraordinary constancy in the course of geological ages; 3. The difficulty of explaining the forms of gynandromorphic ants; and 4. The adaptive characters of soldiers and of workers. Space does not permit even a summary of this discussion here and its result is confessedly an *impasse*.

Thus far the first seven chapters. Of the activities which constitute the social medium of insects the trophic habits alone—owing to lack of time—are considered in Chapter VIII, but they dominate all the others. As "the fundamental nutritive *motifs*" are the leading feature in the book of 1923, its presentation here is less novel than other portions of the present volume. Less novel too are chapters IX and X, on the evolution of the associates and parasites, social and otherwise,

of social insects, which correspond fairly closely to Lecture V of *Social Life among the Insects*, and are indeed in some passages direct translations. In the final chapter (XI. Conclusions) a more extended comparison between insect and human societies is given than is contained in the first lecture of *Social Life*. The future of insect communities is considered in the light afforded by the history of the spread of two ants *Pheidole megalocephala* and *Iridomyrmex humilis* (Argentine Ant). Man will exterminate the terrestrial fauna and flora except that from which he can profit. Ants will long remain his rivals and his torment but they at last will fall before his indirect methods of attack, his modifying or suppressing the external conditions indispensable for their survival.

Les Sociétés d'Insectes, like all of Prof. Wheeler's work, is supplied with an extensive *Index Bibliographique*, here of 40 pages, under authors' names, arranged alphabetically, and then listed under topics, followed by alphabetical indexes of authors and subjects. There are, too, the usual passages at arms with Father Wasmann, which confirm the reviewer's opinion, formed years ago when following the controversial writings of T. H. Huxley and his antagonists, that it is a biological impossibility for two divergent minds to agree.

Prof. Wheeler has fully exemplified all the functions of a University—to preserve, to enlarge and to disseminate knowledge. He has not been content to pursue minute and tedious investigations in embryology, ecology, taxonomy and paleontology, nor with correlating these results with each other and with data drawn from other sciences. He has, on many occasions in books and journals, brought together the noteworthy generalizations of his fields of study, to the edification and—may we not say—delight of those who, like the reviewer, cultivate, with less skill, fewer and more distant acres. *Les Sociétés d'Insectes* is another case in point. Its publication in French will draw attention abroad, not too widely or generously given, to the achievements of American biologists, while it furnishes to all a more up-to-date résumé of the topics of which it treats than any other which we now possess.

BRIEF NOTICES

EVOLUTION

GENESIS *i*. EVOLUTION.
By Reginald Cock. *Elliot Stock*
2 shillings $5 \times 7\frac{3}{8}$; 77 London

The author of this little treatise is a practising physician in London. We take pleasure in presenting him as the second entrant into our *Fundamentalist Portrait Gallery*, reminding our readers that Rudolf Valentino has unfortunately passed away.

Mr. Cock dedicates his book to the memory of "William J. Bryan, Esq." But it must not be inferred from this that Mr. Cock and Mr. Bryan are birds of entirely the same intellectual feathering. They are not quite, although both have equal faith in the infallibility of Holy Writ. Mr. Cock knows more about biology than the silver-tongued statesman ever knew about anything.

But all paradoxers reason queerly, as Augustus De Morgan long ago pointed out. And Mr. Cock is no exception. Thus he says:

Reginald Cock

> Now, it is to Homology and not to Analogy that scientists have been looking, since the evolution theory, in attempting the classification of animals,

and this is a very important matter to bear in mind. Structurally, the lowest animal (amoeba) is below the lowest plant (yeast cell) because the latter has a cell wall, whereas the former has not; yet the animal is without doubt higher functionally.

Common sense and Analogy teach us to group butterflies, birds, and bats together since they all have organs called wings; but Homology induces us to place in one class creatures outwardly so unlike as the rabbit and the whale. This has led to utter confusion and chaos.

Take, for instance, the third section of mammals, called *Monodelphia*, which comprehends all animals which give suck, from porpoises and whales to the monkeys and man. The variation of form presented by the Monodelphian mammals is so great as to defy even their leading characteristics being set forth.

They may be covered with hair or be hairless; they may have a hundred teeth or none at all; they may be gigantic monsters and inhabit the deepest seas.

A very interesting fact to point out here is that the placental method of reproduction is found in certain sharks, as well as in all true mammals. No trace of such a structure exists in any reptile or bird, and it is preposterous to think that the mammals have descended from the sharks. This highly complicated structure must have arisen quite independently in these two instances; and one is at a loss to understand how it could have developed by any process of slow, imperceptible variations, in accord with the evolution theory.

These similar structures, where genetic relationship is out of the question, tend to prove that Homology as a proof of genetic relationship is worthless.

There is Analogy in every Order; and Homology in all corresponding genera.

Every genus descends from a solitary progenitor or primitive couple—called into existence by the direct fiat of a designing Creator; this is why two of every kind, male and female, of every living thing of all flesh were taken into the Ark with Noah (Gen. vi, 19)—with the exception of fishes—in order to preserve the life of every genus. Linnaeus saw the world of organic life as composed of so many well-demarcated types, each separate, distinct, and immutable; each capable of producing its like *ad infinitum* and unable to vary except within very narrow and unimportant limits.

Instead of variability, we see invariability enduring for thousands of years.

What right, therefore, has anyone to assume a constant progress, when the observation of thousands of years, within the historic period of mankind, furnishes no proof of advance?

In the last chapter Mr. Cock answers categorically some of the "posers" (as he calls them) that Mr. Clarence Darrow put to Mr. Bryan at Dayton. Here he scintillates. Bishop Ussher is thrown overboard without a qualm; Cain married one of his sisters, which would now be sinful, but wasn't then; the Flood he approves of; Joshua did not really stop the sun, but did make it hesitate; Jonah was swallowed by *Carcharias vulgaris*.

The book ends with these words: "It is quite possible, and even probable, that the whole battle of Evolution will be fought over again in this country at no remote period, and the evolutionists will find it very much more difficult to substantiate their case once the community have become better informed."

We wonder.

THE EVOLUTION OF LIFE ON THE EARTH.
By Rev. James Morgan.

T. W. Childs and Sons
1 shilling *Teddington, England*
$4\frac{5}{8}$ x $6\frac{7}{8}$; 6 (paper)

This naive little pamphlet, already in a second edition, settles the problem of evolution with a neatness and simplicity which can only command wondering admiration.

On the whole the principle of Evolution of Life on the Earth has been accepted as a natural process. There are, however, two views of this procedure. The one, that of progressiveness, by 'additions' of degrees of betterment; which was adopted by Darwin, and is generally held today. The other, that of the elimination of inferior characters, by what is termed 'Loss.' This means the casting off of the lower grades of life, by emergences from the main life-line.

Darwinism is incomplete. It has not a proper starting point: it assumes that all groups of life have their own special 'ancestors'; but it does not account for the *origins* of those ancestors. It stops before the end, the final purpose, is reached. Nor does it ac-

count for the 'variations' which form an essential element of its method. Take an example—The life-group to which Man and the ape are supposed to belong. It is held, today, that the 'ancestor' of this group is a small animal, *Tarsius*, of the monkey tribe. The origin of this ancestor is not accounted for. The same is affirmed respecting the ancestors of the other life-groups of the Tertiary Period. Nor is the final stage of Man's Evolution explained.

It will be seen that Man has been evolved through the vital principle of his own Main-life-line-strain—and *not* through any order of lower animal life.

The author does not fail to point out that Bateson, in his Melbourne address said: "In spite, therefore, of seeming perversity, we have to admit that there is no evolutionary change which in the present state of our knowledge we can positively declare to be, not due to 'loss.'"

We regret that lack of space prevents the reproduction of Mr. Morgan's entertaining, if not very illuminating, diagram, in which his theory is incorporated.

I BELIEVE IN GOD AND IN EVOLUTION.

By William W. Keen. J. B. Lippincott Co.
$1.25 $4\frac{3}{4} \times 7\frac{1}{4}$; 109 *Philadelphia*

In this fourth edition (eleventh thousand) of this sincere and appealing little tract of reconciliation, its venerable but sprightly author has added new material of three sorts; namely (a), some unimpeachable human tails; (b), an extensive array of evidence as to the similarity between man and animals in the structure of the internal ear; (c), a brief discussion of supernumerary mammae as ancestral vestiges.

THE EVOLUTION OF THE HORSE.

By Frederic B. Loomis. Marshall Jones Co.
$3.00 $5 \times 7\frac{1}{2}$; xvi + 233 *Boston*

A chapter in evolution, well told for the general reader, with excellent illustrations. "The story of the evolution of the horse as revealed by the study of the fossil remains is completed. It is fragmentary and even incomplete at some points, but in general we find a well defined succession of pictures which form a progressive series. The study of palaeontology proves the fact of evolutionary progress in the horse line, but leaves us in doubt about the causes behind it."

GENETICS

COLOUR BLINDNESS. (*Vol. II. Anomalies and Diseases of the Eye. Nettleship Memorial Volume. Part II. Eugenics Laboratory Memoirs XXIII. Francis Galton Laboratory for National Eugenics*).

By Julia Bell. Cambridge University Press
45 shillings $10 \times 12\frac{1}{4}$; 143; *London*
15 plates (paper)

The very high standard which the scientific world has learned to expect in the output of memoirs from Professor Pearson's laboratory is well maintained in this treatise on color blindness. The material is treated under three main heads: Color vision and its anomalies; total color blindness; congenital color blindness. The body of the text is followed by a name index to the chronological bibliography and to the authors of pedigrees, the bibliography which includes 425 titles, the descriptions of the pedigrees, and some 236 pedigrees. The subject is treated with exhaustive thoroughness. The volume will be a reference classic for all time. The chief conclusions regarding inheritance are:

The condition of congenital colour-blindness is strongly inherited and further it belongs to that group of inheritable diseases which is mainly manifested in males and transmitted by their unaffected daughters but not by themselves directly to their

sons. The condition however is not invariable in any single one of these characters and does not appear to conform at all rigidly to the laws of sex-limited hereditary defect of this type.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. Lfg. 182. Containing following articles: *Methoden der Züchtung von Reptilien und Amphibien*, by Paul Kammerer. *Allgemeines über Züchtung von Insekten*, by Franz Heikertinger. *Apterogenea*, by Hans Przibram. *Züchtung der Amphibiotica*, by Franz Heikertinger. *Züchtung von Orthopteren*, by Friedrich Zacher. *Züchtung der Corrodentia*, by Franz Heikertinger. *Züchtung von Rhynchoten*, by Franz Heikertinger.

Urban and Schwarzenberg

9.60 marks 7 x 10; 214 (paper) *Germany*

This number of the Abderhalden handbook will be of especial interest to geneticists because it gives detailed directions for the rearing under controlled cultural conditions of a wide variety of animals.

GENERAL BIOLOGY

A BIPOLAR THEORY OF LIVING PROCESSES.

By George W. Crile. *The Macmillan Co.*

\$5.00 $5\frac{3}{4}$ x $8\frac{3}{4}$; xv + 405 *New York*

Surgeons, or at least some surgeons, have traditionally always loved to philosophize, regardless of the consequences. Considering all the good they have done to suffering humanity in the practice of their proper art, it seems only reasonable that they should be permitted to speculate as much as they like, outside of the operating room and of office hours. Dr. Crile's book needs to be read by biologists with a certain kindly tolerance based upon some such general consideration as has been stated, because it contains an annoying amount of nonsense, along with a lot of interesting and valuable observations. Assuming the existence of such tolerance we recommend the reading of the book. The electrical phenomena associated with vital processes are an interesting and too much neglected aspect of biology, at least in strictly zoological and botanical treatises. The reader of Dr. Crile's book will learn a good deal about them. His thesis, however, that these phenomena are the essential causes of the activities of living things, rather than one of their effects, as pretty well everybody else believes, cannot be regarded as established by the painstaking collection of relevant and irrelevant evidence which he and his colleagues have brought together.

PRACTICAL MICROSCOPY. (*An Introduction to Microscopical Methods.*)

By F. Shillington Scales. *Alex. Eger*

\$2.00 5 x $7\frac{1}{2}$; ix + 332. *Chicago*

An American issue of the third edition of a useful elementary treatise on the use of the microscope. The author is University Lecturer in Medical Radiology and Electrology at Cambridge, England.

DER PARTIALTOD IN FUNKTIONELLER BETRACHTUNG. (*Ein Beitrag zur Lehre von den unspezifischen Reizwirkungen*).

By S. Gutherz. *Gustav Fischer*

3 marks 50 $6\frac{1}{2}$ x $9\frac{1}{2}$; v + 66 (paper) *Jena*

A very interesting, if sometimes speculative, discussion of the biological implications of the Arndt-Schulz law of the beneficial biological effects of minimal stimuli, taken in connection with Weigert's theory of partial death.

ÜBER DEN STOFFWECHSEL DER TUMOREN. *(Arbeiten aus dem Kaiser Wilhelm-Institut für Biologie, Berlin-Dahlem)*
By Otto Warburg et al. *Julius Springer*
16.50 Reichsmark *Berlin*
6 x 9; 263 (paper)

Dr. Warburg, in the *Kaiser Wilhelm Institut für Biologie* in Berlin, is doing some of the most interesting work now going on in the very lively field of cancer research, and it is a great convenience to have brought together in one volume this series of 21 recent papers by himself and his students. It ought also to be said that his researches on cellular metabolism are of quite as great general biological interest, as they are to the cancer specialist.

LIFE AND EVOLUTION. *An Introduction to General Biology.*
By S. J. Holmes. *Harcourt, Brace and Co.*
\$3.50 $5\frac{3}{4}$ x $8\frac{3}{4}$; v + 449 *New York*

The aim of this elementary textbook of general biology is "to present those aspects of biology which would best prepare the student for appreciating the great changes in our outlook upon the world which have resulted from discoveries and generalizations in regard to living forms." This is a commendable idea, and the book is entertainingly written to accomplish the purpose, as would be expected from the author's past performances. The book is extensively illustrated, and has a good index.

THE STREAM OF LIFE.
By Julian S. Huxley. *Watts and Company*
1s 5 x $7\frac{1}{4}$; 56 *London*

This little book constitutes number two of the Forum Series, distributed by the Rationalist Press Association. It consists of eight radio talks on various aspects of heredity, evolution and eugenics, delivered under the auspices of the British Broadcasting Company. The author apologizes in his preface for allowing them to be printed.

AN INTRODUCTION TO PRACTICAL BIOLOGY. *A Course of Work Based Chiefly upon the Plant and Arranged for Use Without Special Apparatus in Either the Classroom or the Home.*
By Norman Walker. *Isaac Pitman and Sons*
\$1.50 5 x $7\frac{1}{2}$; viii + 224 *New York*

A sound and interesting little elementary text book of general biology prepared for the use of adult students enrolled in the Tutorial Class movement in England. The drawings used as illustration are original and largely the work of the students in Adult Classes in Biology. A major part of the space is devoted to plants. The book merits the attention of teachers of evening, extension, and correspondence courses in this country.

L'ACQUARIO MANUTENZIONE FUNZIONAMENTO.
By Felice Supino. *Ulrico Hoepli*
18.50 lire $4\frac{3}{4}$ x $6\frac{1}{2}$; xvi + 201 *Milano*

An excellent, extensively illustrated, little manual of directions for the management of marine and fresh-water aquaria.

A NATURALIST'S PILGRIMAGE.
By Richard Kearton. *Cassell and Co., Ltd.*
7s 6d. 5 x 8; xii +245. *London*

This autobiography of the well-known wild life photographer and lecturer, makes entertaining reading. Kearton's

life has not lacked adventure, and one gets the impression that nothing very important has been lost in the telling. The book is illustrated with nine half-tone plates, some from the author's own superb photographs.

MALIGNANCY AND EVOLUTION. *A Biological Inquiry into the Nature and Causes of Cancer.*
By Morley Roberts.
Eveleigh Nash and Grayson
18 shillings $5\frac{1}{4} \times 8\frac{1}{2}$; 319 *London*

Every biologist should read this book. It contains a wealth of interesting material and valuable suggestions, whether one agrees with the author's views as to the origin of cancer, or does not. The fact that this significant contribution to biological thought is by a professional novelist is not without interest. It develops in novel ways Roux's old idea of the struggle of the parts in the organism.

THE SEASONAL DISTRIBUTION OF THE CRUSTACEA OF THE PLANKTON IN LOUGH DERG AND THE RIVER SHANNON.
By R. Southern and A. C. Gardiner.
The Stationery Office
2s 6d *Dublin*
$6 \times 9\frac{1}{2}$; 170 pp.; xv pls. (paper)

A detailed report upon a quantitative investigation of the plankton in Lough Derg and the mouth of the River Shannon, over a period of three years. While the chief attention is devoted in this report to the Crustacea, data on the phytoplankton, and some of the other elements of the zooplankton, are given.

HUMAN BIOLOGY

AMERICAN VILLAGERS. (*With an Appendix on the Social Composition of the Rural Population of the United States by Luther S. Cressman*).
By C. Luther Fry. *George H. Doran Co.*
\$2.00 $5\frac{3}{4} \times 8\frac{1}{2}$; 201 *New York*

This is an interesting contribution to a neglected aspect of human biology. It attempts to answer, on the basis of a sample of unpublished material in the archives of the Census Bureau, the following questions: "How many villagers are there? Are village populations declining? What kind of people live in villages? What do villagers do for a living? What are the distinguishing peculiarities of village populations? What functions do villagers perform?" The results bring out a number of interesting and unexpected points. About one-eighth of our population lives in villages. Villages are growing in population, not declining. Their population is more largely native white, and has a higher proportion of old persons than do city populations. Their gainfully employed inhabitants are more largely engaged in manufacturing pursuits than anything else, even in a purely agricultural region. Villagers have poor medical service. The statistical method used involves what amounts to a pretty heavy extrapolation, and one should be cautious about accepting detailed conclusions. There is no index.

HOW NATIVES THINK. (*Les Fonctions Mentales dans les Sociétés Inférieures*).
By Lucien Lévy-Bruhl. *Alfred A. Knopf*
\$4.00 $5\frac{3}{4} \times 8\frac{1}{2}$; 392 *New York*

It is a distinct service to have this anthropological classic available in English. The essential thesis of the book is

the formulation of what the author calls the "law of participation" to explain the workings of the minds of primitive peoples. Regarding their "law" Professor Lévy-Bruhl says (p. 76):

> At the moment it would be difficult to formulate this law in abstract terms. However, in default of a wholly satisfactory formula, we can make an attempt to approximate it. I should be inclined to say that in the collective representations of primitive mentality, objects, beings, phenomena can be, though in a way incomprehensible to us, both themselves and something other than themselves. In a fashion which is no less incomprehensible, they give forth and they receive mystic powers, virtues, qualities, influences, which make themselves felt outside, without ceasing to remain where they are. In other words, the opposition between the one and the many, the same and another, and so forth, does not impose upon this mentality the necessity of affirming one of the terms if the other be denied, or vice versa. This opposition is of but secondary interest. Sometimes it is perceived, and frequently, too, it is not.

The author devotes a great deal of space to bowling over Tylor's "animism" theory. But there are perhaps just as great, though different, weak spots in his own. However it is an important contribution to have emphasized and worked out the sociological factor in primitive thought with the shrewdness and skill that Professor Lévy-Bruhl has brought to bear on what must always remain an extremely complex and difficult problem.

DIE HYGIENE DER MENSCHLICHEN FORTPFLANZUNG. *Versuch einer praktischen Eugenik.*

By Alfred Grotjahn. Urban and Schwarzenberg
15 Marks 7 x 10; xi + 344 (paper) *Berlin*

This treatise by the professor of social hygiene at the University of Berlin, takes the sound position that if eugenics is ever to be practical it must concern itself with *groups*, that is populations, rather than with individuals. There is nothing that can be done to alter the hereditary constitution of an individual, whether it be good or bad, so far as anything now known in genetics demonstrates. But the hereditary constitution of a group or population, taken in a statistical sense, can obviously be altered, and this is done every day in laboratories of genetics with populations of lower organisms. Grotjahn devotes his book to a painstaking and thorough assembling of the data necessary for the formulation of a scientific program of group eugenics, or racial hygiene. It constitutes a useful reference work.

MEDICAL AND EUGENIC ASPECTS OF BIRTH CONTROL. *Vol. III.*
RELIGIOUS AND ETHICAL ASPECTS OF BIRTH CONTROL. *Vol. IV.*
Edited by Margaret Sanger.
American Birth Control League, Inc.
\$2.00 each. $5\frac{1}{2} \times 8\frac{3}{8}$; $\begin{cases}247\text{ (paper)}\\240\text{ (paper)}\end{cases}$ *New York*

In the third volume of proceedings of the 1925 Birth Control Conference are papers by fourteen medical persons, and eight biologists. Mainly they have only ephemeral value. The most significant contributions appear to be those by Dr William Allen Pusey, and Dr. S. Adolphus Knopf.

The fourth volume contains twenty-eight papers, by as many different authors. Generally they deal with the vaguer humanistic aspects of the birth control movement. Three of the papers make significant contributions, these are "Conduct as a Science," by Professor Harry Elmer Barnes; "Problems of hedonistic sex relations," by Professor Adolf Meyer; and "The population problem in India," by Dr. Taraknath Das.

CONSERVATION OF THE FAMILY.
By Paul Popenoe. *Williams and Wilkins*
$3.00 5⅝ x 8; 258 *Baltimore*

This book is a piece of propaganda for a number of theses maintained by a small group of eugenists in this country. Scientifically its value, if it has any at all, is trifling. While operating in a different field of discourse its intellectual outlook and exegetical technique exactly parallel those of William Jennings Bryan and John Roach Straton in regard to religion and evolution, or of Irving Fisher and Howard A. Kelly in regard to prohibition.

LES RACES ET LES PEUPLES DE LA TERRE.
By J. Deniker. *Masson et Cie.*
$3.00 6½ x 10; 745 (paper) *Paris*

The manuscript of the second edition of a classical anthropological text, first issued more than a quarter century ago, was practically ready for the printer when the author's lamented death occurred. By arrangement between the publishers and M. Deniker's family, parts of it have been edited and prepared for publication by various French specialists. It constitutes an excellent general text book of anthropology and ethnology.

RACE AND HISTORY. *An Ethnological Introduction to History.*
By Eugene Pittard. *Alfred A. Knopf, Inc.*
$6.50 6 x 9; xxiii + 505 *New York*

This volume in the History of Civilization series, written by the distinguished professor of anthropology at the University of Geneva, is intended as a companion and supplement to Febvre's *Geographical Introduction to History* in the same series. This develops the racial factor, in the sense of physical anthropology, whereas Febvre attempts to evaluate the environmental factor. Pittard's book is a solid, substantial contribution. It constitutes the best existing summary of the broad human meaning and significance of the wealth of detailed information which physical anthropology has accumulated. There is a bibliography of 300 titles and a detailed index.

DAS WACHSTUM DES KINDES.
By Eugen Schlesinger. *Julius Springer*
6 marks 7 x 10; 127 (paper) *Berlin*

A detailed and thorough critical review, with a bibliography of over 300 titles, of the literature on human growth, together with some original investigations by the author himself in this field. It is a reprint from Vol. 28, of the *Ergebnisse der inneren Medizin.* It will be a valuable reference work.

PREHISTORIC MAN AND THE CAMBRIDGE GRAVELS.
By Rev. Frederick Smith.
W. Heffer and Sons, Ltd.
7s.6d. 5½ x 8½; viii + 121 *Cambridge*

This most entertaining book should be read by everyone interested in human pre-history, and who nowadays is not. For it is a wonderful record of enthusiasm and imagination brought to bear upon inherently unexciting material, chunks of flint from gravel pits. For more than 60 years the author has been collecting and studying what he believes to be the very earliest paleolithic worked flints, and trying by imagination and experiment to figure out how they were used and what for. It is greatly to be feared that his

conclusions will not be accepted in their entirety by the hard-boiled experts in prehistoric archeology. But his book is great fun, and he might be partly right. And his casualness is superb. Out of ten arrowheads on one plate he says that "three or four were culled from gravel in the Pepys Court of Magdalene College, two from paths in Trinity, and two from King's."

ALCOHOL AND LONGEVITY.
By Raymond Pearl. *Alfred A. Knopf, Inc.*
\$3.50 $5\frac{1}{2} \times 8$; xi + 273 *New York*

The author now publishes in book form the results of his investigations, extending over a number of years, of the effect of alcohol upon the duration of human life. The general result is that moderate drinkers show no impairment of longevity as compared with total abstainers. Heavy drinking materially shortens life. The experimental literature on the racial effect of alcohol is reviewed. This is a bibliography of 269 titles.

QUELQUES CONSEILS POUR VIVRE VIEUX.
By Maurice de Fleury. *A. Michel*
9 francs $4\frac{3}{4} \times 7\frac{1}{2}$; 304 (paper) *Paris*

A treatise on personal hygiene, containing much shrewd advice and a minimum of quackery. The author appears not to be a fanatic entirely opposed to all the pleasant things of life, as advisers about personal hygiene are too apt to be. On the contrary he preaches a doctrine of moderation, which general experience would indicate to be sound.

ZOOLOGY

BIRDS IN ENGLAND. *An Account of the State of Our Bird-Life and a Criticism of Bird Protection.*
By E. M. Nicholson. *Chapman and Hall*
12 s. 6 d. $5\frac{1}{2} \times 8\frac{3}{4}$; xix + 324 *London*

This extraordinarily interesting and original book deals systematically with the ecological relation between birds and men in the British Isles at the present time. The discussion hinges about bird protection. The author demonstrates with great wealth of detail what idiotic mistakes zealous but ignorant uplifters can make. Two long chapters on the balance of the bird population, with an analysis of the reasons for the alterations in the proportionate numbers of different species, constitute a first rate contribution to evolution theory. There is an excellent index, and a list of the scientific names of all birds mentioned in the text. Finally must be mentioned the eight beautiful woodcuts by E. Fitch Daglish with which the book is illustrated. They have high artistic value.

LES MOLLUSQUES D'EAU DOUCE. (*Encyclopédie Pratique du Naturaliste XXIV*).
By E. Chemin (Preface by L. Joubin).
Paul Lechevalier
25 francs $4\frac{1}{2} \times 8$; 185, 15 plates *Paris*

An excellent little handbook which introduces the reader to the fresh-water molluscs in the happiest possible way. It takes up successively all of the genera found in France. Under each genus the most common species is first discussed in considerable detail, as to its structure, its physiology, its mode of life, habits, etc. Then the other species of the genus are described with sufficient detail so that

they can be easily identified with the help of the illustration. The whole is very well done, and results in a book which has real charm, and will inevitably attract young people who chance to read it to observe and perhaps really study fresh-water molluscs. Why do we not do this sort of thing in this country? The whole effort of biological teaching here seems to be to make the subject as forbidding and unattractive as possible, by talking about nothing but physics, chemistry and mathematics, and by confining the student strictly to a dingy laboratory.

MARVELS OF REPTILE LIFE.
By W. S. Berridge.
Thornton Butterworth, Ltd.
6 s $5\frac{3}{4}$ x 9; 256 *London*

For the "marvellous" purposes of this book and the series to which it belongs, amphibians are counted as reptiles. The author excuses this on the ground that the book "does not purport to be a scientific treatise." It is in fact a pleasantly written popular bit of natural history, well illustrated by half-tone plates of photographs, most of which seem to be original and to have been made in a zoological garden. The author makes some very up-stage remarks about the palatability of the diamond-back terrapin, which the editorial staff of The Quarterly Review of Biology, as loyal denizens of the Maryland Free State, cannot allow to pass unchallenged.

PERSONALITY OF WATER-ANIMALS.
By Royal Dixon and Brayton Eddy.
Brentano's
\$2.50 6 x $8\frac{1}{4}$; xxv + 254 *New York*

An abundantly and well illustrated hodge-podge of cheap natural history writing about animals that live in water. The book has no unity or coherence, and the depth of its philosophy is sufficiently indicated by the following quotation:

> Perhaps some day we shall learn that Fishes are but undeveloped birds, that the Garden of Eden was a submarine garden and Adam and Eve had scales and fins. Then, perhaps, we shall look upon our lesser brethren more sympathetically. The greatest of all teachers—Christ—knew the value of marine education for he chose as his disciples men thoroughly acquainted with the sea.

BIOLOGIE DER TIERE DEUTSCHLANDS. (*Lieferungen* 7–14).
Edited by Paul Schulze *Gebrüder Borntraeger*
$5\frac{1}{2}$ x $8\frac{3}{8}$ (paper) *Berlin*

Lief. 7, 1.80 Marks, 100 pp.
Hymenoptera I. By H. Bischoff.
Amphibia. By A. Remane.
Lief. 8, 1.80 Marks, 94 pp.
Hymenoptera II. By H. Bischoff.
Lief. 9, 1.65 Marks, 69 pp.
Ephemoptera. By Georg Ulmer.
Reptilia. By A. Remane.
Lief. 10, 1.80 Marks, 70 pp.
Plecoptera. By Ed. Schoenemund.
Coleoptera I. By H. v. Lengerken.
Lief. 11, 1.65 Marks, 64 pp.
Nematodes. By Gerhard Wülker.
Lief. 12, 1.95 Marks, 68 pp.
Coleoptera II. By H. v. Lengerken.
Lief. 13, 3.60 Marks, 113 pp.
Trichoptera. By Georg Ulmer.
Lief. 14, 2.55 Marks, 68 pp.
Euphyllopoda. By H. Spandl.
Bryozoa. By Ernst Marcus.

The high standard set in the earlier numbers of this collected work, already noticed in The Quarterly Review of Biology, is well maintained in the numbers here listed. When completed the whole will make a valuable reference work.

A NATURALIST'S NOTE-BOOK IN CHINA.
By Arthur De Carle Sowerby.
North-China Daily News and Herald
Mex. $8.00 $6\frac{1}{2} \times 9\frac{3}{4}$; 270 *Shanghai*

With the exception of a few early chapters this popular treatise on the natural history of China deals exclusively with animals lower in the scale than mammals or birds. The book is eminently readable, and contains a good many interesting original observations. It makes no attempt at scientific profundity, but is just a pleasant general survey of the lower animal life of China. The book is quite extensively illustrated with photographs and line drawings, the latter mostly by the author himself. There is no index.

I MOLLUSCHIE E LE CONCHIGLIE.
By Carlo Piersanti. *Ulrico Hoepli*
48 lire. $4\frac{1}{2} \times 6\frac{1}{4}$; xiv + 527 *Milano*

This manual first discusses in a series of introductory chapters the general biology, anatomy, physiology and ecology, of molluscs and then follows with a systematic portion for the identification of the Italian species. The work is well done, and will surely prove a useful aid to beginning Italian zoologists. There is an extensive bibliography, a good index, and 403 illustrations. It is unfortunate that each separate half-tone cut is outlined by an ugly black border.

THE HISTORY OF PROTOZOOLOGY.
By F. J. Cole. *University of London Press*
3 shillings $5\frac{1}{2} \times 8\frac{3}{4}$; 64 *London*

This book is made up of two charming lectures on the history of our knowledge of Protozoa, delivered at the University of London. The author stirs the reader's curiosity and desires by saying "these lectures are based on material for a general history of Zoological Discovery which I have been collecting for many years." This general history of zoology will be eagerly awaited, now that so tempting a sample has been furnished. There is a bibliography of some seven pages.

THE ANT. (*A Popular Account of the Natural History of Ants in all Countries.*)
By Edward Step. *Hutchinson and Co.*
7s. 6 d. 6 x 9; xii + 276 *London*

A compilation, to some extent from first-hand sources, of information about the biology of ants, for popular consumption. The book is abundantly illustrated with half tone plates. There are no specific bibliographical citations. The author seems to have but a meager first-hand acquaintance with American literature on the subject. There is an index.

BRITISH SPIDERS. *Their Haunts and Habits.*
By Theodore H. Savory.
Oxford University Press
$2.00 $4\frac{3}{4} \times 7\frac{1}{4}$; xii + 180 *New York*

The first six chapters of this well written little handbook deal with the general biology of spiders, their anatomy, and the principles of their taxonomic characters. The remainder of the book is devoted to descriptions, with fairly well worked out keys for identification, of the species most commonly found in Great Britain. The book is sufficiently illustrated, mostly with original line drawings, and is well indexed. One chapter is devoted to directions for keeping spiders in captivity.

DIE GIFTPRODUKTION BEI DEN TIEREN VON ZOOLOGISCH-PHYSIOLOGISCHEN STANDPUNKT. (*Zugleich ein Hinweis auf funktionelle Beziehungen zwischen Giften, Hormonen, Gerüchen*).
By J. Strohl. *Georg Thieme*
2 marks $6\frac{3}{4}$ x 10; 56 (paper) *Leipzig*

A reprint in separate form of a series of papers by the Swiss zoologist Strohl which amount to a *Sammelreferat* of what is known about the production of poisons by animals, unified by the point of view that poisons are mainly by-products of the normal physiologic-metabolic economy, and may have important functional relations and uses besides being poisonous to other animals.

TIERISCHES LEUCHTEN UND SYMBIOSE. (*Vortrag gehalten in der Zoologisk-Geologiska Foreningen zu Lund am 5. October 1925.*)
By Paul Buchner. *Julius Springer*
2 marks 70 $5\frac{3}{4}$ x $8\frac{1}{2}$; 58 (paper) *Berlin*

This lecture assembles and discusses evidence in support of the thesis that light-producing animals cultivate, in their special phosphorescent organs, luminous bacteria, which are passed on from generation to generation "like a holy flame." There is a brief bibliography of literature relating to symbiosis and bioluminescence.

A PRACTICAL HANDBOOK ON RAT DESTRUCTION.
By C. Leopold Claremont. *John Hart*
3s. 6d. $4\frac{3}{4}$ x $7\frac{1}{4}$; 180 *London*

The chief reliance of this treatise is upon poisoning. Extensive directions are given for its practical employment. The book is an outcome of the Rats and Mice (Destruction) Act, which was passed by Parliament in 1919, and marks at any rate the beginning of a systematic attempt of the English to get the upper hand of these pests.

IL NATURALISTA VIAGGIATORE
By Gestro E. Vinciguerra. *Ulrico Hoepli*
14 lire. $4\frac{1}{2}$x 6; xv + 204 *Milano*

A little handbook for the field naturalist which gives directions for collecting, labelling, and preserving specimens. There is unfortunately no index. A translation of this book, with some editing for American conditions, would be a useful aid to our students.

DAS PROBLEM DER ZELLTEILUNG PHYSIOLOGISCH BETRACHTET.
By Alexander Gurwitsch. *Julius Springer*
16.50 marks $5\frac{1}{2}$ x 8; vii + 218 (paper) *Berlin*

This volume serves the useful purpose of bringing together in summarized and unified form the results of the author's investigations, extending over many years, on the physiology of cell division. Some enterprising American publisher should arrange for an English translation of this book.

THE CATTLE GRUBS OR OX WARBLERS, THEIR BIOLOGIES AND SUGGESTIONS FOR CONTROL. (*U. S. Department of Agriculture Bulletin No. 1369*).
By F. C. Bishopp, E. W. Laake, H. M. Brundrett, R. W. Wells.
Government Printing Office
25 cents *Washington, D. C.*
6 x 9; 119 (paper)

A thorough and detailed account of the biology of the two economically important species of *Hypoderma*. There is a

bibliography of 112 titles. This bulletin is the record of a fine piece of research in natural history.

BOTANY

STUDIES IN ADVANCING STERILITY.
Nos. 1 and 2. Part I. The Amherstieae. Part II. The Cassieae.
By John McLean Thompson.
University of Liverpool Press
4 s. 6 d. each *Liverpool*
$8\frac{1}{4}$ x 12; No. 1, 54 (paper)
No. 2, 47 (paper)

The general purpose of the first of these extensively and beautifully illustrated morphological memoirs from the Hartley Botanical Laboratories of the University of Liverpool is

> to illustrate from the floral development of members of the *Amherstieae*, a tribe of Caesalpinoid *Leguminosae*, the importance of a knowledge of ontogeny in any systematic discussion, and the light which it may throw on the problems of a group as a whole. From the evidence adduced it is held that the chief problem with which the *Amherstieae* are faced in the ontogeny of their flowers is an advancing sterility of their androecium. The entire tribe is held to be evolving towards total sterility, by perversion to petaloidy, or by complete inhibition, of the primordia of the stamens.

There is a bibliography of eighty-eight titles.

The second memoir proceeds along similar lines to the first. In the *Cassieae*

> that sterilisation of the gynoecium has occurred and still occurs is accepted on the evidence for *Cassia* itself, though the single carpel which is typical of the tribe seems remarkably stable. On the other hand it has been shown that while complete sterilisation of the gynoecium is typical of one genus, with separation of the sexes, it is occasional in another without any apparent biological advantage being attained. The tribe as a whole is therefore held to be evolving towards total sterility, by perversion, arrest and inhibition of the primordia of its essential floral organs.

There is a bibliography of fifty-seven titles.

BAKTERIEN-CYCLOGENIE. (*Prolegomena zu Untersuchungen über Bau, geschlechtliche und ungeschlechtliche Fortpflanzung, und Entwicklung der Bakterien.*)
By Günther Enderlein. *Walter de Gruyter*
20 marks $6\frac{3}{4}$ x 10; viii + 390 (paper) *Berlin*

In this book the distinguished entomologist of the Zoological Museum of the University of Berlin enters upon a new and widely different field, the life cycle of bacteria. He states that the book was written in substantially its present form in 1915–16, apparently with the idea of delicately but firmly establishing priority over Löhnis, who published his first important paper in this field in 1916. The book starts with a brief historical review of the literature on the morphology of bacteria. This is followed by descriptive sections on the comparative cytology and general morphology of bacteria, based upon the author's own work, and illustrated by scale drawings. Then follows a chapter on the reproduction asexual and *sexual* of bacteria. This leads to a long section on the life cycle of bacteria. The remainder of the book deals with such questions as classifications, infectious diseases, etc., in the light of the author's discoveries and conclusions. Finally there is (a) an index of the new findings, (b) a bibliography, (c) a complete chronological list of all of the author's own publications, 285 in number, and (d) a general index. A new and somewhat bewildering terminology is invented and used throughout. But the talk is of new facts, if they are facts, so new words are excusable.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. Lfg. 186. Containing the following articles. *Die Bestimmung der Titrationsacidität in Pflanzenextrakten und ähnlichen gefärbten Flüssigkeiten. Die Bestimmung des formoltitrierbaren Stickstoffes in Pflanzenextrakten und ähnlichen gefärbten Flüssigkeiten. Die Bestimmung präexistierender Substanzgruppen (Säure, formoltitrierbarer Stickstoff, Kohlehydrate usw.) in Pflanzen*, by Heinrich Leurs. *Nachweis der Assimilation des Luftstickstoffes*, by Alfred Koch. *Methoden zur Bestimmung der Aufnahme organischer Stoffe durch die höhere Pflanze*, by Walter Kotte. *Methoden zur Bestimmung der Assimilation der Kohlensäure aus der Luft und aus dem Wasser*, by Heinrich Schroeder.

Urban and Schwarzenberg

4.80 marks 7 x 10; 102 (paper) *Germany*

Details of technique in the study of plant metabolism, particularly on the biochemical side.

THE STUDY OF VEGETATION.

By E. Pickworth Farrow.

Blackie and Son, Ltd.

2 s. $4\frac{7}{8}$ x $7\frac{1}{4}$; 23 (paper) *Glasgow*

This pamphlet is a reprint of an article in *Discovery* which had for its purpose to arouse popular interest in the study of ecology. It is well done.

LIFE OF PLANTS.

By Sir Frederick Keeble.

Oxford University Press, American Branch

\$1.75 5 x $7\frac{1}{2}$; xii + 256 *New York*

The distinguished professor of botany at Oxford, adds, by this volume, to his already distinguished reputation as a writer of popular biology. In brief space, and with great clarity and real literary distinction, it gives an account of the essentials of plant morphology and physiology, including genetics. The book is well illustrated and indexed and we recommend it highly to the general reader, as well as to the teacher and beginning student.

THE PHYSIOLOGY OF PLANTS. *The Principles of Food Production.*

By George J. Peirce. *Henry Holt and Co.*

\$3.00 $5\frac{1}{2}$ x $8\frac{1}{2}$; x + 363 *New York*

A treatise on plant physiology which follows novel lines, at least in the general philosophical viewpoint from which the well-known subject matter is approached, and according to which it is arranged. We strongly commend the book. It is readable. It is scientifically sound. It is no dreary, dull compilation, as at least nine-tenths of all the biological text books which go over this editorial desk are. It has *Geist*.

A LABORATORY GUIDE FOR GENERAL BOTANY.

By C. Stuart Gager.

P. Blakiston's Son and Co.

\$1.25 $5\frac{1}{4}$ x $7\frac{3}{4}$; x + 203 *Philadelphia*

The third edition of a well-known and thoroughly established set of laboratory directions for a course in general botany.

COURS DE BOTANIQUE, *à l'usage des établissements de l'Enseignement moyen.*

By O. Terfve and P. Turlot.

Ad. Wesmael-Charlier

50 cents $5\frac{3}{4}$ x $8\frac{3}{4}$; 341 *Namur*

This book is a masterpiece of tedium, containing no fact discovered since 1875 and no theory proposed since 1850. The

plant kingdom is described as if it were embalmed. Each chapter is headed by the portrait of a Belgian botanist; throughout the text no others are mentioned; but the poor Belgian child who is taught from this frightful work will not be led to follow in their footsteps. Doubtless a translation would suit the purposes of the Tennessee Board of Education.

ÉTUDES FLORISTIQUES SUR LA RÉGION DU LAC SAINT-JEAN. *Contributions du Laboratoire de Botanique de l'Université de Montréal, No. 4.*
By Frère Marie-Victorin.
Université de Montréal
$1.00 6 x 9; 174 *Montreal*

A local floral list.

EINE BOTANISCHE TROPENREISE. (*Indo-Malaiische Vegetationsbilder und Reiseskizzen*).
By G. Haberlandt. *Wilhelm Engelmann*
9.50 marks $6\frac{1}{4}$ x 9; x + 296 *Leipzig*

This is the third edition of a classical treatise on tropical vegetation, first issued in 1893. The text is little changed from its original form, though, as the author points out, the conditions of travel and of botanical work in Java have greatly changed in thirty-five years. The book remains a delight, however.

CATALOGUE OF THE PRINTED BOOKS ON AGRICULTURE PUBLISHED BETWEEN 1471 AND 1840 WITH NOTES ON THE AUTHORS.
By Mary S. Aslin.
Rothamsted Experimental Station Library
10 shillings 6 x $9\frac{3}{4}$; 331 (paper) *Harpenden*

A fine piece of bibliographical work, which will stand as a solid contribution to the history of agriculture. The book will be found useful for reference by historians of botany and, to a lesser extent, zoology.

MORPHOLOGY

LOGIK DER MORPHOLOGIE IM RAHMEN EINER LOGIK DER GESAMTEN BIOLOGIE.
By Adolf Meyer. *Julius Springer*
18 Reichsmark *Berlin*
$6\frac{3}{4}$ x 10; vi + 290 (paper)

There is no getting around the fact that this is a dull book. We have struggled with it on several occasions, and emerged each time more depressed than before. It is not that there is anything wrong with it. Every statement seems unimpeachable. But 279 pages of precise discussion of the logical implications of the working definitions and procedures of biology is not only a lot, but also is steadily, ineluctably, and devastatingly *boring*. For anybody, if there is such a person, who likes this sort of thing, this is a good book. But our guess is that it will not make much difference in the conduct of any biologist's life.

THE COMPARATIVE ANATOMY, HISTOLOGY, AND DEVELOPMENT OF THE PITUITARY BODY.
By. G. R. de Beer. *Oliver and Boyd*
12s. 6d. $5\frac{1}{2}$ x $8\frac{3}{4}$; xix + 108 *Edinburgh*

This volume in the series of *Biological Monographs and Manuals* edited by Crew and Cutler, is a careful piece of straight morphological research on the pituitary

body. Following an introductory chapter on technique the structure and development of the pituitary is followed through the great animal groups from mammals to cyclostomes. The book is illustrated by eleven plates (some colored) and one hundred and eighteen drawings in the text. There is a bibliography covering four pages and an index. It will be a useful reference book.

OUTLINES OF COMPARATIVE ANATOMY OF VERTEBRATES.

By J. S. Kingsley. P. Blakiston's Son and Co.
$4.00 6 x 9; x + 470 *Philadelphia*

The third edition, considerably revised, of Kingsley's standard textbook. The bibliography has been brought down to date. It is an excellent text and its past success should be continued in this new edition.

MORPHODYNAMIK. *Ein Einblick in die Gesetze der organischen Gestaltung an Hand von experimentellen Ergebnissen. Abhandlungen zur theoretischen Biologie, Heft 23.*

By Paul Weiss. Gebrüder Borntraeger
2,70 marks $6\frac{3}{4}$ x 10; 43 (paper) *Berlin*

A philosophical—and in some degree metaphysical—discussion of the problems and data of experimental morphology. This address will particularly interest those who are struggling with the emergent evolution doctrine.

HISTOIRE DE L'ANATOMIE COMPARATIVE.

By J. Chaine. E. Daguerre
24 fr. $5\frac{1}{2}$ x 8; vi + 461 (paper) *Bordeaux*

This stout volume forms the historical portion of a large work on comparative anatomy, of which one previous volume has appeared, and two more are announced. The author, who is a professor of the Faculty of Sciences, at Bordeaux, proceeds in a pleasant leisurely way, with much philosophical discussion, written in a beautifully clear style. The book is a welcome addition to the meager literature on the history of zoology. It is well indexed.

PHYSIOLOGY

BIOLOGICAL RELATIONS OF OPTICALLY ISOMERIC SUBSTANCES.

By Arthur R. Cushny.
The Williams and Wilkins Co.
$2.00 $5\frac{1}{2}$ x $8\frac{1}{2}$; ix + 80 *Baltimore*

This third series of lectures of the Charles E. Dohme Memorial Foundation at the Johns Hopkins Medical School constitutes a welcome addition to a neglected field of pharmacology, and, more broadly, of general biology. The untimely death of Professor Cushny, so soon after these lectures were delivered, has left a real gap in the scientific world. His sound, deep scholarship and ripe wisdom were never more clearly shown than in these lectures. Their broad biological significance is indicated by the following concluding remarks:

> I have dwelt at what may have appeared to you prodigious length upon the properties of optical isomers in living tissues, because it seems to me that here we have a clearer connection between the behaviour of substances in the test tube and in the living tissues than is often met with. For I think it is beyond question that the differences in the reaction of the two components of atropine on the salivary glands on the one hand and to such substances as camphor-sulphonic acids on the other are of the same essential nature, each depending on the union of two optically active substances. We have seen that they are conditioned in part by the asymmetry, in part by some specific configuration including the presence of

HO; of these, asymmetric carbon is present in every organ and cell, but the configuration necessary for the development of its results is limited to very few organs. The reaction is so definite when it is present that it may be taken as a test for the presence of this configuration in the tissues.

TIERPHYSIOLOGISCHE ÜBUNGEN.

By Paul Krüger. *Gebrüder Borntraeger*
30 marks *Berlin*
7 x 10½; xxv + 518 (paper)

This is a combined text and laboratory guide for a comprehensive course in general physiology. If the work called for is done with any thoroughness at all, there would be required at least a year's course of three laboratory periods a week. The author states that he has never been able to get it all into one semester. The course starts with some physical chemistry, followed by some physiological chemistry. Then the vital phenomena themselves are tackled, *Reizphysiologie*, *Stoffwechselphysiologie*, etc. There is nothing novel in this plan, nor in the book. It is simply a well developed course along lines which have been standard and conventional in the teaching of general physiology in this country for some twenty years past.

THE FURTHER STUDIES ON DECREMENTLESS CONDUCTION.

By Genichi Kato. *Nankōdō*
6 x 9; 163 *Tokyo, Japan*

This is a detailed report of a series of investigations by the author, who is professor of physiology at Keio University, and his students, in further elaboration and support of his conclusions that:

1. The *intensity* of nervous impulse does not suffer decrement during passage along the narcotised region of nerve. 2. The *rate* of the nervous conduction suffers no decrement during the passage along the narcotised region. 3. The nervous impulse of *subnormal intensity* (for instance the nervous impulse evoked in the relatively refractory period) suffers no decrement during conduction along the narcotised region of nerve. 4. The nervous impulses of *varying intensities* are extinguished at the *same* stage of narcosis, that is the intensity of nervous impulse has no influence at all on its ability to travel through the narcotised region of nerve. 5. The *all or none principle* is valid in the narcotised region of nerve. It must be noted that the quantity of 'all' (the size of maximal response) becomes gradually less as the narcosis deepens, but at any stage of narcosis the size of nervous impulse is not dependent on the strength of stimulus applied, it gives always the maximal response possible in that stage of narcosis or none at all. 6. The nerve loses by narcotisation its excitability and conductivity at the *same* time.

Thus, according to the new theory of decrementless conduction, the nerve suffers no *qualitative* but only quantitative change by narcotisation, whereas the old theory of decrement maintains that not only narcosis but also any other abnormal condition of nerve bring about qualitative change (decrement and inapplicability of all or none law).

MORE LIGHT. *A Simple Account of How the Brain Works.*

By Sidney Cameron.
Williams and Norgate, Ltd.
3s. 6d. 5 x 7½; xiii + 75 *London*

This is an original and interesting speculation. Its conclusions, with most of which probably no biologist will agree, are as follows:

The brain is an organ for generating and distributing nerve energy. The energy is derived from the blood, and stored in a chemically unstable form in the grey cells of the cerebral hemispheres, medulla, and spinal cord. The distribution to the muscles and organs is effected through the nerve filaments. All nerves are efferent, that is, the flow of energy is in one direction from the centre to the periphery. The optic, the auditory, the dental, the tactual nerves offer no exceptions to this rule. In all cases the nerves convey outgoing currents, which impart muscular or sensory tonus to the sense organs or

muscles. The body, which includes the brain and nervous system is primarily a neuro-muscular organism. Perceptions and memories are as extraneous to it as the reflected light which illumines the inert body of the moon. Memory is not to be explained by the morphology of the brain cells, but is a phenomenon that is deducible from the nature of space-time. By assuming appropriate attitudes, and by suitable adjustments of the muscular system, particularly those parts of it which are concerned in the production of speech, the body is able to pick up signals from the past, and thus reconstruct it in idea with the aid of mental and verbal imagery.

THE SECRETION OF THE URINE.
By Arthur R. Cushny.
Longmans, Green and Co.
$5.50 $5\frac{3}{4}$ x $8\frac{3}{4}$; xii + 288 *New York*

This second edition of Professor Cushny's well known treatise in the series of *Monographs on Physiology*, appeared only after his death, but fortunately he had read the galley proofs, so that as Professor Starling says in a note, it puts "on record his considered views on a subject in which his theory serves at the present time as the starting-point for all the work that is proceeding in different laboratories." Much new material has been reviewed in this edition. Over 200 titles have been added to the bibliography, which now totals to 593 references. The book is well indexed and will long serve as a standard reference source.

TRAITEMENT DES MALADIES MENTALES PAR LES CHOCS.
By C. Pascal and Jean Davesne.
Masson et Cie.
60 cents $5\frac{1}{4}$ x $7\frac{1}{2}$; xv + 182 (paper) *Paris*

Stimulated probably by the recent successes in treating general paresis with malaria, the authors have brought together in this little book much of the literature on the use of the many substances which have from time to time been injected into the veins of the sick with the hope of startling them into recovery. Unfortunately, no attempt has been made to evaluate the methods described, to sum up what has been accomplished, or to give the experience of the writers, so one is left with the impression of having read little more than a plan on paper.

LA SÉCRÉTION INTERNE DU PANCRÉAS ET L'INSULINE.
By André Choay. *Masson et Cie.*
$2.00 $6\frac{1}{4}$ x $9\frac{1}{2}$; xx + 570 (paper) Paris

A thorough-going review of the physiology of the pancreas, documented with a bibliography of 1377 titles. The book is divided into four parts: Historical résumé of the period before the discovery of an internal secretion of the pancreas; experimental diabetes and the demonstration of the existence of an internal secretion; pancreatic extracts now employed therapeutically under the name insulin; physiology of the internal secretion of the pancreas. A supplementary chapter deals with the reciprocal relations between the pancreas and other endocrine glands. The book is well indexed.

CARBOHYDRATE METABOLISM AND INSULIN.
By John J. R. Macleod.
Longmans, Green and Co.
$6.00 $5\frac{3}{4}$ x $8\frac{3}{4}$; xii + 357 *New York*

The purpose of this monograph is stated by its distinguished author, the co-discoverer of insulin, to be "to give a

comprehensive review of the advances which have been made in our knowledge of the metabolism of the carbohydrates during recent years, and more especially since insulin became available. This is preceded by an account of the researches which led up to the isolation of this hormone and a review of the evidence that it is derived from the Isles of Langerhans of the pancreas. The nature of the diabetic condition which supervenes upon withdrawal of insulin from the body is also discussed." It is needless to state that the treatment is thorough and exhaustive. Extensive bibliographies follow each of the twenty-one chapters. There is a detailed index.

STUDIES IN INTRACRANIAL PHYSIOLOGY AND SURGERY. *The Third Circulation. The Hypophysis. The Gliomas. (The Cameron Prize Lectures, delivered at the University of Edinburgh October 19, 20, 22, 1925).*
By Harvey Cushing. *Oxford University Press*
\$3.25 *American Branch, New York*
$6\frac{1}{8} \times 9\frac{7}{8}$; xii + 146 (paper)

The first of these delightful and epoch-marking lectures deals with the cerebrospinal fluid and the spaces through which it circulates. The second treats of the pituitary body and its disorders, while the third discusses brain tumors in general and the gliomas in particular. The lectures are followed by bibliographies of 70, 49, and 62 titles respectively, these lists being limited to the papers of the author, his students, and their students. The whole forms a record of consistent first-rate research achievement, of which all concerned may well be proud. The volume is sparsely but significantly illustrated, and well indexed.

BIOCHEMISTRY

BIOCHEMIE DES MENSCHEN UND DER TIERE SEIT 1914. *Wissenschaftliche Forschungsberichte. Band XII.*
Edited by Felix Haurowitz.
Theodor Steinkopff
7 marks $6 \times 8\frac{3}{4}$; xii + 148 (paper) *Dresden*

A condensed conspectus of the progress of biochemistry—on the animal side—since 1914, which gives individual references to more than eleven hundred bibliographical titles. It makes a very useful reference work.

CERTAIN ASPECTS OF BIOCHEMISTRY.
By J. C. Drummond, A. V. Hill, H. H. Dale, and L. J. Henderson.
University of London Press
12s. 6d. $5\frac{1}{2} \times 8\frac{3}{4}$; viii + 313 *London*

This volume prints thirteen lectures given in the University of London in the summer session of 1925, by four distinguished physiologists and biochemists. The lecturers and subjects treated are as follows: Dr. H. H. Dale, The Chemical Control of Certain Bodily Functions: I, The Control of the Circulation in the Capillary Blood-vessels; II, Active Principles of the Pituitary Body; III and IV, The Pancreas and Insulin. Prof. J. C. Drummond: I and II, Modern Views on the Mechanisms of Biological Oxidations; III, Certain Aspects of the Rôle of Phosphates in the Cell; IV, The Vitamins. Prof. L. J. Henderson: Blood and Circulation from the Standpoint of Physical Chemistry: I, The Physico-chemical Changes in Blood during the Respiratory Cycle; II, The Synthetic Description of Blood as a Physico-chemical System; III, Deductions concerning the Circulation. Prof. A. V. Hill: I, The Physical Environ-

ment of the Living Cell; II, Lactic Acid as the Keystone of Muscular Activity.

The book as a whole is a notable performance. It serves as a very readable, and at the same time authoritative, bird's-eye view of recent progress in nearly all of the more lively fields of physiology. All of the authors maintain a high level of excellence in their treatment of their respective subjects, but Prof. L. J. Henderson's section deserves especial mention as a masterpiece of bold and successful scientific generalization, popularly expounded with consummate skill.

SEX

GESCHLECHTSLEBEN UND FORTPFLANZUNG DER ESKIMO. (*Abhandlungen aus dem Gebiete der Sexualforschung, Band IV, Heft 6*).
By Hans Fehlinger.
A. Marcus und E. Weber's Verlag
RM 2 $6\frac{3}{4}$ x $10\frac{1}{4}$; 36 (paper) *Bonn*

A useful compilation from the literature of what has been recorded regarding various aspects of the biology of reproduction and of sex among the Eskimos. The material is discussed under six heads, as follows: General remarks about the Eskimo; marriage; morality; pregnancy, parturition and rearing of the child; fertility; race-crossing. There is a bibliography of 23 titles. The observations upon which the treatise is based are, in the nature of the case, mainly rather casual and scattered. Putting them together as Fehlinger has done shows where the great gaps in our knowledge are, regarding this basically important branch of human biology in such an anthropologically significant group of people as the Eskimos.

MODERN MARRIAGE.
By Paul Popenoe. *The Macmillan Co.*
\$2.50 5 x $7\frac{1}{2}$; xiii + 259 *New York*

Detailed directions as to how to get a wife and how to keep her. Nothing whatever is left to either imagination or instinct. The chapter on courtship, entitled "How?" is wonderful.

FORTSCHRITTE DER SEXUALWISSENSCHAFT UND PSYCHANALYSE. *Band II.*
Compiled by Dr. Wilhelm Stekel; Edited by Dr. Anton Missriegler and Emil Gutheil.
Franz Deuticke
18 marks *Leipzig*
$6\frac{1}{4}$ x $9\frac{1}{4}$; iv + 575 (paper)

This is a voluminous and depressing record of bad dreams and sad case histories. The volume includes thirty-three papers, and a few book reviews. The only amusing one we have been able to find in the lot is a learned disquisition upon Martin Luther's scatological tendencies, and even here there is a strenuous, though unsuccessful, attempt to preserve the prevailing psychoanalytic gloom. Probably all these papers, with their abundant technical terminology, are good science, and therefore to be approved of, but it is difficult to refrain from inquiring "good for what?"

KÖRPER UND KEIMZELLEN. *Teilen I und II.*
By J. W. Harms. *Julius Springer*
33 marks (each) *Berlin*
$5\frac{1}{2}$ x 8; x + 516 und 508 (paper)

A thorough, detailed, well illustrated review of the extensive literature on the relation between the gonads, secondary sexual characters, and the general structural and functional economy of the body.

It is a welcome and useful addition to the literature of general biology. The author is professor at Tübingen. There is a bibliography covering forty-eight closely printed pages, and an index.

BIOMETRY

MEASUREMENTS OF THE CUBICAL CONTENTS OF FOREST CROPS. *Being a Critical Investigation into the Methods of Measuring Sample Plots with Special Reference to the Liability to Error. Oxford Forestry Memoirs No. 4.*
By M. D. Chaturvedi.
Oxford University Press
\$3.50 *American Branch, New York*
$7\frac{1}{2}$ x $10\frac{3}{4}$; xv + 142 (paper)

This detailed mathematical discussion of the measurement of the volume of an individual tree, and of the total volume of wood in a forest stand, is chiefly of interest to professional foresters. All of the different methods which have been suggested are critically reviewed. None appears to have more than somewhat unprecise relative accuracy. There is a bibliography covering about four and a half pages.

SUR LES SEMI-INVARIANTS ET MOMENTS EMPLOYÉS DANS L'ÉTUDE DES DISTRIBUTIONS STATISTIQUES. *Skrifter utgitt av Det Norske Videnskaps-Akademi i Oslo. II. Hist.-Filos. Klasse 1926, No. 3.*
By Ragnar Frisch. *Jacob Dybwad*
7 x $10\frac{3}{4}$; 87 (paper) *Oslo*

Treats of the relations between the semi-invariants, moments, and factorial moments of frequency distributions, and of the use of generalized Bernoulli numbers in dealing with these parameters. The binomial and hypergeometric distributions are considered in detail.

PSYCHOLOGY AND BEHAVIOR

THE MEANING OF PSYCHOLOGY.
By C. K. Ogden. *Harper and Brothers*
\$3.00 $5\frac{1}{2}$ x $8\frac{1}{2}$; xxi + 326 *New York*

This is a popular *résumé*, in the simplest language possible, of the present state of knowledge and opinion in the field of psychology. The author's purpose is primarily exposition rather than conversion to any particular doctrine. With shrewd critical insight he steers a happy course among the warring isles of the psychologic archipelago, and gives the voyager a fine view of the pleasant scenery on each, without subjecting him to any dangers or hardships at all. The popularity of the book is well deserved. It has an excellent index.

INTELLIGENCE AND IMMIGRATION.
By Clifford Kirkpatrick.
Williams and Wilkins
\$4.00 6 x 9; xiii + 127 *Baltimore*

This volume, which constitutes the second number in a series of *Mental Measurement* monographs, first summarizes the results of other investigators in so-called intelligence testing of different race stocks in this country, and reaches the conclusion that these studies have shown that "in general the representatives of the newer immigration, especially the Latins, have less intelligence than the Americans or those of the older immigrant stock." There then follows a detailed account of the author's own investigation of a group of Massachusetts school children falling into the following groups: French Canadians, Finns, Italians, and Americans.

The tests used were the "Illinois Examination," and the Army Beta. The following conclusions were reached:

> Americans are but slightly, if at all superior to the Finns in intelligence. Both are far above the Italians, and the French Canadians, taken as a whole, rank between these two extremes. These differences are accentuated by a linguistic handicap. The demonstration of a linguistic handicap means that these important differences in intelligence are less than they appear, but it fails to disprove their existence.

There is a bibliography of 146 titles and an index.

BRAINS OF RATS AND MEN.
By C. Judson Herrick
University of Chicago Press
\$3.00 $5\frac{1}{4} \times 7\frac{1}{4}$; xiii + 382 *Chicago*

This book is a serious attempt to develop a consistent view of human psychology and personality upon a groundwork of what is known of the morphology of the vertebrate nervous system. In this latter field the author is an acknowledged master. Therefore his views, on the philosophical, and to some extent metaphysical questions which this attempt implies and involves, are entitled to a respectful hearing. They are extremely interesting, if perhaps not always fully convincing. There is a bibliography of thirteen pages, and an index.

TELLING ON THE TROUT.
By Edward R. Hewitt.
Charles Scribner's Sons
\$2.50 $5\frac{3}{4} \times 8\frac{1}{4}$; xi + 166 *New York*

An enthusiastic fisherman contributes a good deal more than the expected expert advice about flies, rods, and other tackle. Mr. Hewitt has made many original observations on the habits and behavior of different species of trout in various parts of the world. Also he has carried out some interesting observations and experiments on the vision of fish. The book is a worthy addition to the ecological and behavioristic library. It unfortunately lacks an index.

IS NATURE CRUEL? *A Partial Answer to the Question. Experiences of Big Game Hunters and Others While Under the Attack of Wild Beasts.*
By J. Crowther Hirst. *G. Bell and Sons*
1 shilling $4\frac{1}{8} \times 6\frac{5}{8}$; 61 (paper) *London*

This little book defends the odd thesis that the killing of living things for food by predatory animals, particularly the large carnivora, is neither a particularly painful nor fearsome process for the killed. The evidence adduced is the testimony of various persons who have been mauled by lions, tigers, and bears, or have witnessed such maulings, to the effect that they did not feel much pain at the time. It is a curious book, now in a second edition.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

THE MILLENNIUM AND MEDICAL SCIENCE.
By David Nicholas Schaffer, M.D.
Wilbur Needham
\$2.00 $5\frac{1}{2} \times 8$; 371 *Evanston, Ill.*

On pages 356, 357, and 358 of this "Wonder Book of the Age" is one single sentence containing 509 words, by actual and time-consuming count. We believe this is by no means the longest sentence in the book. We only counted this one because we got lost in it, both subject and predicate escaping our clutches together. This unfortunate stylistic char-

acteristic of a book warmly recommended by publishers and author to

(a) Those who have read "Black Oxen," and
(b) Those who have not read "Black Oxen,"

makes it a little difficult to follow the plot though there are many nice, sonorous words, fairly printed on a medium quality of paper. Chapter XIX is entitled "The Theory." We have carefully read it through six times. But regretfully we are obliged to say that we cannot find out what the theory is. To our dull perception there seems to be nothing in the chapter but an involved and verbose recital of some of the elementary facts of the physiology of human reproduction, with a lot of mostly erroneous drivel, about hormones, enzymes, vitamines, glands, and bacteria. The book has some diagrams, but all attempts to capture the big idea by Mark Twain's formula of "treeing it in the pictures" have failed. The one bit of real entertainment derived from this welter of stupid dullness is to be found in a diagram lying between pages 140 and 141, which carefully distinguishes between the "Arterial Blood Stream" and the "*Venus* Blood Stream" *in the pelvic region*. Thus proving that "God's in his heaven," etc.

A DICTIONARY OF MODERN ENGLISH USAGE.

By H. W. Fowler. Oxford University Press
$3.00 5 x 7½; viii + 742 *New York*

This book is a joy. While dictionaries are not popularly supposed to make good reading, this is an exception. It is replete with sly humor and entertaining quips. At the same time it is the most thorough and authoritative treatise which exists in compact form on the difficulties and niceties of the English tongue. Everyone who does any writing, and particularly every scientific man, should have this enormously useful book constantly at his elbow.

INTRODUCING REGINALD

The increasing complexity of our editorial life has made it necessary for us to employ an office boy. His name is Reginald. He is young, but exhibits the shrewdness usual in the lower anthropoids. We have considerable hope that he may be trained to do the necessary simple tasks of the office.

But he has already shown a disturbing, though characteristic, mischievousness. As the last page proofs of this number were going to the printer Reginald slipped in the following contribution, which he says he made up with scissors and paste from things he found lying about on the editorial desk.

Debate About Evolution

PRO

Coming now to the evidence afforded by systematic zoology as to the course of evolution, we see at once that inferences from it involve a rather dangerous assumption. This assumption is that some species stood still and retained the ancestral form and habits whilst allied species became modified. Nevertheless there are many cases in which this assumption appears to be sound. Squirrels, whose form and habits are familiar to all, are very much alike wherever they occur all over the world; the Canadian squirrel is especially familiar to Londoners as it has been introduced into the Royal Parks and is rapidly multiplying. It can often be seen leaping from branch to branch in Kensington Gardens. But in Canada there exists another and rarer variety, the so-called flying squirrel, which has a parachute-like expansion of skin reaching from the knee to the elbow. This squirrel is capable of taking colossal leaps of seventy to eighty yards in length during which it "volplanes" through the air supported by its parachute. Does anyone doubt that this species has been developed from the normal type by becoming continually adapted to making longer leaps? Thus systematic zoology can show what course evolution

has followed in the case of an isolated species amongst the other species of a genus, when the majority have a uniform type of structure and habits, and the same reasoning applies to an isolated genus amongst the normal genera of a family

The reasoning becomes much more doubtful when we ascend higher in the scale, because it becomes more difficult to be sure that one family or one order has remained unmodified and can be taken as representing ancestral structures whilst others have changed.

The case of the flying squirrel, however, raises another question which is of far-reaching significance. This squirrel lives to-day in the very same woods as those inhabited by the common squirrel: yet the latter appears to thrive quite as successfully as the flying squirrel. The peculiarities of the flying squirrel must therefore have arisen in a different region, where trees were sparse and where it was exceedingly dangerous to descend to the ground, but having evolved its peculiar habits there it has spread into more normal situations.

(By Professor Ernest W. MacBride, F.R.S. in "*Evolution in the Light of Modern Knowledge*," pp. 250–252, 1925.)

CON

I noticed recently that a cow, while grazing, used her tail vigorously to drive away the flies. I began to think as to how I should account for the existence of cows' tails, if I were an evolutionist. In the early stages of the development of cattle, of course they would be tailless. When their bowels moved there was left at the opening a small deposit of fecal matter. This attracted the flies. In order to get rid of the flies the animal twitched the flesh at this part of the body. This was continued for many generations till it resulted in a protuberance as a permanent feature of cattle. Continued stretching of this protuberance to drive the flies from other parts of the body caused it to lengthen, and after a few millions of years the tail became a universal character of the species. Additional vertebræ were added to the dorsal column, and the caudal appendage developed into its present proportions.

But in my evolutionary thinking I struck a snag: If the cow's tail was developed by use, why should it have stopped at its present dimension? The cow stretches her tail in vain toward her shoulders and her head. The flies are especially busy about her eyes, but she cannot brush them off with her tail. According to the evolutionist, we may assume any length of time we may think necessary; but with all the billions of years at our disposal, the shortness of the cow's tail, as long as it is, proves that evolution is an error.

Again I noticed that the tail of the horse, though the two animals subsist on similar food and grew up in similar environment, is very different from the tail of the cow. The vertebræ in the cow's tail are nearly uniform in size from end to end, while those of the horse are smaller and smaller toward the outer end. Moreover the cow has a bunch of long hair, somewhat like a paint brush, at the end of her tail, while the horse's tail has long hair from end to end.

I have wondered too at the supposed development of the rattles on the tail of the rattle-snake. According to the evolutionists there must have been a time when the snake had no rattles. If he attempted to rattle without success, is it likely that he would continue to try to rattle for a sufficient number or generations to have made the rattles come? The snake's tail is even more difficult to account for under the theory of evolution, than the cow's.

(By W. R. Coppedge in the Charlotte, North Carolina, *Observer*.)

Reginald has been reprimanded.

VOL. II, NO. 2 JUNE, 1927

THE QUARTERLY REVIEW *of* BIOLOGY

NERVE AND MUSCLE

BY MARION HINES

Department of Anatomy, Johns Hopkins University

IN THIS review of the present status of investigations upon the relation of nerve to muscle, the writer will consider only that of skeletal muscle. Exact knowledge of the termination of nerves on the smooth muscle and heart muscle fiber has progressed little in the last twenty-five or thirty years. Although both the parasympathetic and the sympathetic innervate these two types of muscle, nothing is known about the relation of these two divisions of the autonomic system to individual muscle elements (Woollard's (1926) excellent monograph on heart muscle contributes nothing to this particular aspect of the question). The only instance in which the particular endings of the autonomic system have been distinguished in their relations to individual cellular elements is the recent study of Stormont (1926) on the submaxillary gland of the rabbit. If this same type of work were to be extended to the innervation of other glands and in particular to heart muscle and smooth muscle, we should have an interesting anatomical basis for certain physiological peculiarities. Here, however, the questions of plurisegmental innervation, the type of fiber in skeletal muscle, the muscle spindle or sensory organs of muscle, the motor endings, and finally a discussion of the recent papers on the mooted question of tonus, particularly in its relation to the nerve endings, will be considered.

PLURISEGMENTAL INNERVATION

In an investigation of the muscles innervated by the *N. medianus* and *N. ulnaris* in domestic animals, Agduhr (1915) found that the sum of the contractions resulting from the maximal stimulation of each nerve separately as seen in *M. flexor digitorum sublimis* and the lateral portion of the humoral head of the *M. flexor digitorum profundus* was greater than the contraction obtained by the simultaneous maximal stimulation of both nerves together.

In the cat the *M. flexor digitorum sublimis* is innervated by the 7th and 8th cervical and the 1st thoracic nerves. Agduhr (1916) cut the 1st thoracic nerve 90 hours, and the 7th cervical 58 hours before killing the animal, allowing the 8th cervical to remain sound. He found

that the same muscle fiber might be innervated by both the 7th and the 8th cervical. It happened that in all muscle fibers having two motor end plates, one of them showed degeneration. In 1919 he cut the ventral roots in the cat at C_7, 96 hours and Th_1, 192 hours before sacrifice of the animal and examined the *M. interossei* with Bielschowsky's technique. In another animal C_7 was cut 96 hours, and C_8 168 hours, before the animal's death. In a few instances the same muscle fiber showed that it was innervated by C_7, C_8 and Th_1; but the majority were bisegmentally innervated. On the other hand, Floresco (1903) and Cavalié (1901) on purely morphological grounds have described motor fibers giving off terminal filaments to two or more motor end plates in the same muscle or to adjoining muscle fibers or muscle spindles.

Such a peculiar morphological finding as that of Agduhr could not remain unchallenged long. In 1924, Cattell and Stiles found that on stimulating separately each of the nerve roots to the frog's gastrocnemius the sum of tension developed in an isometric tetanus exceeded in the ratio of 1.7 to 1 the tension developed when the entire sciatic nerve was stimulated. They concluded that about 70 per cent of the fibers have double segmental innervation. Katz in the same year studied the heat developed by stimulating the two components of the sciatic nerve separately and together and found it to be the same, within the limits of experimental error. There is, then, in his estimation no plurisegmental innervation of frog's muscle. De Boer (1926) studied the action current of the same muscle in the frog and thought that the monophasic deflection was the same whether the *N. viii* and *N. ix* were stimulated separately or together.

Fulton (1925) studied the gastrocnemius of *Rana temporaria*, innervated by *N. viii* and *N. ix*, by measuring simultaneously the plateau tension and the electrical response. Although the result of a simultaneous stimulation in both cases was less than the sum of separate stimulations, and the difference varied in the same direction in both cases, nevertheless, the percentage of variation was two to three times greater in tension than in electrical response. Therefore, he believes that the amount of tension produced is not necessarily a real criterion for plurisegmental innervation.

Such a dilemma can only be resolved by an actual study of the muscle itself. We should know definitely about its innervation and then study its physiological behavior. As far as the writer knows, there are no morphological studies on the gastrocnemius muscle but from studying the sartorius after section of *N. ix* in the frog it is quite clear that many of its fibers are plurisegmentally innervated.

RED AND WHITE MUSCLE

In Cobb's (1925) recent consideration of the tonus of skeletal muscle and in Needham's (1926) review, the histology of red and white muscle is adequately discussed. However, as some understanding of the essential differences between these two types of muscle is necessary, a brief discussion of the salient observations will be given. Hunter (1925, p. 13) reopened this old question when he suggested "that the skeletal muscle of vertebrates consists of two sets of muscle fibers disposed in groups, each with its own specific innervation, and consequently, its own specific function." He believed that the fibers receiving the somatic innervation were similar to the "movement muscle" of invertebrates and that those innervated by the sympathetic nervous system resembled the fixing muscles in that they

remained at the new length imposed upon them. Such a broad generalization would be of fundamental importance were it true. As is evident it must not only be made to rest upon physiological evidence but its strongest prop is to be fashioned out of histological findings.

It does not take a trained scientist to discover that the meat of vertebrates varies in color; that of fish, amphibians and reptiles is more or less colorless while that of birds and mammals may vary from white to deep red. This difference in color was at first thought to be due to a greater blood supply found in some muscles than in others. But Kühne (1865) after carefully washing out the vessels of red muscles, prepared water extracts of the minced substance. He examined the absorption spectrum of such a preparation and thought the pigment to be hemoglobin. For further confirmation he prepared certain derivatives of hemoglobin such as hematin, CO-hemoglobin, and reduced hemoglobin from the extract. In 1872 Lankester published a paper upon the distribution of hemoglobin in the animal kingdom, paying particular attention to it as it is found in invertebrates. In some he found it as a free pigment in the body fluids and in one as a pigment of the head ganglion. In *Limnaeus* and *Paladina* (1871) he found that the muscles of the pharynx contained a pigment which was spectroscopically identical with hemoglobin. He concluded in general that hemoglobin was found in those places where either the oxidation processes were rather rapid or had to be performed in the absence of an oxygen supply easy of access. Also it was found in those muscles where prolonged activity was required. Recently Keilin's (1925) studies on the properties of certain animal and plant pigments have substantiated this older work. For instance, he demonstrated that the red muscles of the guinea-pig show two bands of HbO_2 when exposed to air, which do not correspond exactly with those of HbO_2 from the blood of the same animal. In the pigeon the alpha band of HbO_2 of muscle is 5805, that of blood, 5763. However, these two pigments are as similar in the same animal as hemoglobin itself is when one species is compared with another. When the pectoral muscles of the pigeon are used for this study it is necessary to add a very dilute solution of KCN, in order to break up the oxidation system of the tissue—certainly a finding pregnant with implication for the physiology of red muscle.

The gross appearance of these two kinds of muscle is particularly striking when the white pectoral muscles of the domestic chicken are compared with the dark red of the goose, duck and pigeon or of birds which are relatively infatigable in flight like the buzzard or falcon (Starling, 1920). Although Meyer (1875) was able to confirm Ranvier's (1873) finding that the adductor of the rabbit was white and the semitendinosus was red, he found that such muscles as the *flexor digitorum communis* and the masseter which were red muscles had the histological characteristics of the white. There appears even after the exhaustive studies of Knoll a great difficulty in making any adequate generalization as to the distribution of red and white muscle. Starling (1920) is perhaps correct that all striated muscle of higher vertebrates contains both types of muscle fibers, and but few muscles are almost exclusively red or white. In man, where the distribution appears to be more mixed than elsewhere (Roberts, 1916), the muscle fibers of an athlete are not only larger in diameter than those of the ordinary man but also redder (Morpurgo, 1897). The minute histology of such a

change has not been studied as far as the writer is aware,—that is, we do not know whether the increase in redness is due only to the increase in size of the red fiber, with corresponding increase in the amount of pigment, or whether some of the white fibers also contain pigment. Were the latter true the morphological differentiation would not appear as great.

These two types of muscle fibers may be distinguished morphologically as well as spectroscopically. The amount of sarcoplasm is relatively greater in the red muscle fiber. Its nuclei are not always found immediately beneath the sarcolemma, as is true for the white muscle fiber, and the diameter of the red is much less than the white. Meyer (1875) described the overlying sarcolemma as brighter and the oval nuclei as lying in a finely granular sarcoplasm. Schaffer (1893) reported for man that the clear sarcoplasmic or white fibers contained small myofibrils arranged rather regularly, while in the granular sarcoplasm or red fibers, the myofibrils are large and the arrangement without order.

In 1883 Grützner published studies on the histology of these two fibers. He thought that the more granular fibers were similar to the red and that the less granular, or larger clear fibers corresponded to the white. A few years later Knoll spoke of them as protoplasm-poor and protoplasm-rich fibers. Such fibers, not distinguished by a content of pigment, make up the skeletal musculature of amphibians and reptiles. Grützner studied in particular those of the frog, where all are white in color except the superficial ones of the neck (and of course the heart). The smaller fibers, that is, those poor in protoplasm, contain granules which according to Knoll stain with the osmic acid of Flemming's fluid, and are reddened by the gold salt in the Ranvier technique. Krause suggested that the smaller of these two types of muscle fibers, together with a third, smaller in diameter than the other two and having its nuclei in the center, were stages in the development of the large fiber. Then Bonhöffer studied the distribution of these three types at various ages and found that they appeared in about the same numbers.

In recent unpublished studies upon the intercostal and neck muscles of the newborn sloth, Wislocki (1926) has observed that the myofibrils of all the fibers are exceptionally large and their bands broad and especially distinct. They are so loosely spaced in the sarcoplasm that the cell appears to be longitudinally striated. The nuclei are larger and found more often near the periphery of the fiber than its center. The sarcoplasm is not as granular as that which lies about the centrally placed nucleus of the granular fiber in the muscle of *Amblystoma*. Rather it is quite similar to the small fiber of the frog. In the recently dead adult, all the muscles of the limbs vary from red to deep red or to reddish brown. None of them appear white. The histology as far as known certainly classifies the muscles examined as red. In no other mammal so far studied has red muscle dominated.

The writer has studied certain muscles of the frog, the sartorius, the gastrocnemius and the *pectoralis abdominalis*. If these three muscles are watched in isotonic salt solution under oil immersion or high power, the first difference which appears between the three types of fibers is one of diameter and nuclear arrangement. As the study is continued the middle sized fiber becomes very granular; the longer it remains, the more granular it becomes. If, however, the muscles are fixed through the circulation with either Bensley's (1911) acetic-osmic-bichromate mixture

or with formalin Zenker, there is no difference in granulation. It is quite true, as Knoll observed, that these granules are reddened by gold chloride; but when the fixative is quick in its action after death, there are no granules which blacken in osmic acid. The very small fibers of Krause do not show these granulations. This is the fiber of the muscle spindle, the intrafusal fiber of Sherrington (1894).

If the muscle is allowed to stand an hour or more following the intravascular injection of methylene blue, the small fibers turn blue first, then the intrafusal fibers and sometimes the larger or clear fibers are slightly tinted. In cross sections of the whole leg of the frog, the diameter of the fibers of its individual muscles varies tremendously. The cross dimension of the large fibers in the sartorius is almost the same as that of the smaller ones in the gastrocnemius. It is quite clear that the distinction in size holds within an individual muscle but size alone cannot remain a criterion, when another muscle is considered. However, it is always the smaller fiber within a given muscle which grows granular upon death, has its nuclei scattered through the sarcoplasm and stains with methylene blue. Bonhöffer (1891) thought that the white muscle could reduce methylene blue faster than the red. Ahlgren (1921) found for the rabbit's chopped muscle that the reduction limit is much less for red muscle using the methylene blue technique. These two findings are not necessarily contradictory, for the cytological changes appear to take place sooner in the granular than in the clear muscle, not only the fiber but also its nuclei being colored. To the student of living tissues this is a criterion of death and subsequent permeability. The initial time of the reduction of methylene blue to the leuco-base may be shorter in the case of the red than the white and yet the red may die sooner.

Further, there is no difference in the distribution or size of the mitochondria or of the glycogen granules in the two types of muscle fiber in the frog. There was no extra-nuclear iron, as judged by Bensley's Prussian blue reaction, nor was any hemoglobin present as determined by MacCallum's method (1890). Keilin (1925) using another method, also found no hemoglobin in frog muscle. The cytoplasmic method (MacCallum, 1890) for the detection of phosphorus was not used. After Bensley's (1906) careful study of this technique, it appears almost worthless. Were the method more reliable it might be possible to detect a microchemical difference in the phosphorus content between the white fiber and the red. Gross chemical methods have demonstrated the white muscle to contain more than the red (Needham, 1926). If these methods could be applied microchemically it might aid in determining whether or not the clear fibers and the granular fibers of lower vertebrates were similar to the white and red fibers of birds and mammals.

Besides their differences in morphology and chemistry red and white muscles are distinguished by certain individual physiological peculiarities. Ranvier (1875) demonstrated for the first time that it took more stimulations per second to produce a continuous contraction in white muscle than in red. Later he found the length of twitch shorter in the white fiber, the latent period one-fourth as long, the tetanus much less, the fatigue greater, and the after-tetanus excitation much less than in the red fiber. This was followed by Grützner (1883) who showed that red muscle contracted more slowly and had a

longer latent period. Adrian (1925) says that

> the time-relations of the contraction are much slower in red muscle than in white, so that a red muscle fiber should be able to give a sustained contraction with a much smaller energy expenditure than a white. But the contractions are of essentially the same type in the two and the electric response of red muscle has the usual form, though it is slower in development and decline.

Cobb and Fulton (1925) confirmed the earlier work, namely, that the electrical response of white muscle is more rapid than red and that its latent period is shorter. In addition, they showed a prolonged flat top in the curve of the red muscle. They concluded, and rightly, that its contraction does not resemble smooth muscle. This prolonged contraction of the red muscle is beautifully demonstrated by the work of Hay (1901) in his comparison of the contractions of the semimembranosus with the soleus in the rabbit in response to a single break shock through the sciatic with and without curare. He found also as might be expected that ligature of the blood vessels affected pale muscle more than red. Reflex excitation by pinching the tibial nerve at the ankle elicitated a vigorous and rapid reflex contraction of the semimembranosus with little or no response from the soleus. After strychnine the former was exaggerated: the latter, irresponsive.

Contrary to Hay's results on the rabbit, Fischer (1908) in comparing the action of the gastrocnemius with the soleus in the cat found only a negligible difference in the latent period. The twitch of the soleus was higher than the gastrocnemius and, like Hay's finding, the time of contraction was longer. The curve for the isometric twitch is prolonged for the soleus, and is slightly higher than that for the gastrocnemius. A frequency of 80 stimuli per second is necessary for the gastrocnemius to attain a smooth tetanus of a height (54 mm.) comparable to that (53 mm.) which the soleus reaches with 13 per second; the time of development for the former is one second, for the latter, three; but strangely enough, the height for the white muscle at the beginning of tetanus is almost three times that of the red (40:15 mm.). In an isometric twitch the gastrocnemius reaches a tension of 600 gm., in isometric tetanus 700 gm. for a relatively short time; on the other hand, with the soleus the tension of isometric twitch is 200 gm., but with repeated stimuli it can maintain a tetanus of 950 gm. for a long time. It is interesting that the relative tension given by Hay after a stimulus of a single break shock was of the same ratio of 3 to 1, i.e., 150 gm. to 50 gm. for the semimembranosus and the soleus of the rabbit. In the other laboratory animals studied by Fischer, the rabbit, rat and guinea-pig, variations between the red and white muscles were in the same direction as those in the cat with one exception, namely, the soleus twitch was never so high as the gastrocnemius.

Roberts (1916) found, in the rabbit, that the red fiber degenerated if anything more rapidly following section of the nerve to the muscle,—a finding quite opposed to what would be expected from Hay's demonstration that the lack of blood supply affected the red less than the white. He was unable to compare the reaction of degeneration of these two types of muscle, partly because of the difficulty of isolating the soleus from the gastrocnemius and maintaining at the same time its blood supply, and partly because of the varied development and atrophy of the soleus. He believed that the anatomical relations of red muscles such as the soleus, the crureus and the deep head

of the triceps are not without significance. If they entered into contraction simultaneously, the elbow, knee and ankle would be in a position resembling decerebrate rigidity. Red muscles usually unite adjacent segments of the limb while white muscles often pass over one or more joints. In such cases he believed that fixation of one joint is carried out by the deeper lying red muscle. But in man, the red and white fibers are not separated in particular muscles but combined in every muscle. "It is common knowledge that man is capable of performing movements of graded intensity." Those two facts may be associated as Roberts believed or they may not. He thought that the red fibers play a prominent rôle in the maintenance of posture, that they perform slow and gradual movements, that they act synergically with white muscle in the fixation of one joint so that another may be moved.

There is no fundamental anatomical difference in the innervation of these two types of muscle in the rabbit. The motor end plates were the same size and constituted in the same manner. Hay found that the semimembranosus weighed 7.1 gm. and the number of nerve fibers to it were about 4187: the soleus weight was 1.28 gm. and the fibers numbered 787—a ratio by weight of 5.6 to 1 and by number 5.3 to 1. In the osmic acid preparations the white muscle nerves varied from 15 to 18μ, the red from 10 to 13.5μ. He could discover no difference in the muscle spindles. After section of the 7th, 8th and 9th posterior thoracic roots the ratio of undegenerated nerves remained about 5 to 1. The only difference which appeared was in size of the nerve fiber and the thickness of the myelin sheath. Very recently, Feldberg (1926) has studied the auricular muscles of the rabbit after monolateral sympathetic denervation. No difference was noted between large and small fibers on the two sides.

It is rather striking that the color of skeletal muscle in birds and mammals with few exceptions may be correlated with the histological structure of the fiber itself; and perhaps still more so that this minute anatomical differentiation of muscles predominately either red or white should parallel difference in their physiological behavior. A physiological study of these exceptional muscles like the *flexor digitorum communis* and the masseter of the rabbit, which Ranvier found to be red in color but similar to the white in structure, might lend a suggestion for the function of the hemoglobin content of the red muscle fiber. By means of such an investigation, negative though it must be, some concept of the physiology of the large sarcostyle and its surrounding granular sarcoplasm might be reached.

The comparative study of the structure of muscle fibers of vertebrates other than birds and mammals has not demonstrated any particular muscle as composed more or less completely of either granular or non-granular fibers. Consequently, the physiology of such nerve muscle preparations as that of the gastrocnemius of the frog may not be compared with any justification to that of either red or white muscles in mammals or birds. The investigator is dealing with a muscle as mixed in type as the majority of those of higher vertebrates. So long as no differences in innervation of red and white fibers or of the granular and non-granular can be discerned with our present technique, the cause for their dissimilarity may be considered to lie in the structure of the fiber itself. This situation is further complicated by a finding in the frog (anticipating data presented on the motor innervation) that the same axis cylinder may divide and end hypolem-

mally in motor end plates of similar morphology upon a granular and a non-granular fiber. If for the pleasure of discussion the results of the study of the physiology of white and red fibers of mammalian forms be transferred respectively to the non-granular and granular fibers of certain reptiles and amphibians, a new difficulty raises its head, namely, the same nervous impulse must be translated by the two kinds of muscle fiber into types of contraction signally different, and the quality of activity of these two muscles would then be a function of their structure alone.

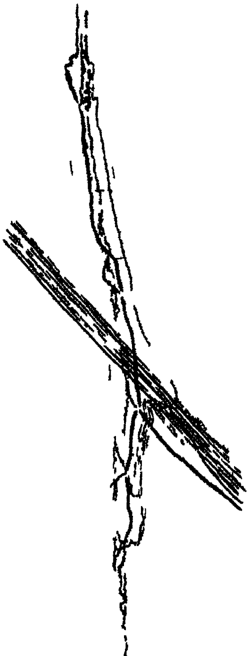
MUSCLE SPINDLES

The term "muscle spindle" is a translation of *Muskelspindel*, first used by Kühne (1863) for the small muscle fibers, spindle-like in form, found more or less encapsulated in the connective tissue septa of the skeletal muscles of higher vertebrates. In all forms they are shorter than the muscle fibers which make up the major part of the muscles. The separation of these elements from the rest of the muscle tissue varies greatly. In mammals, the intrafusal fibers are surrounded by a perilymphatic space, which Sherrington pleased to call periaxial, limited by a thick connective tissue capsule. No such space is found in birds or reptiles or tail-less amphibians. Muscle spindles have not been found by the older workers (Kerschner, 1888; Giacomini, 1898; Baum, 1899) in fish nor in the tailed amphibians (Franque, 1890; Giacomini, 1898). As far as the writer knows, no work has been done since that time. Although there may be no spindles as such it is highly probable that some sensory mechanism exists. But what, is not known.

The interest in this subject was renewed by the work of Kulchitsky (1924) on the muscle spindles of the python (Plate 1, fig. 1). The writer wishes to give a brief résumé of the relation of the nerves to these structures as far as they are known at the present time beginning with amphibians. We shall consider the work on reptiles in detail, comparing their structure with that of birds and mammals. There is quite a variation, which may account for the difference in the physiological results reported for removal of different parts of the nervous system. These data with those which will be presented for other innervation of the skeletal muscle argue for a certain restraint in the presentation of generalizations for all vertebrates, resting upon morphological findings in the muscle innervation of one form.

The muscle spindles of the frog, or fascicles of Weismann, contain a variable number of muscle fibers grouped together. Franque (1890) described an insignificant connective tissue capsule lying about the area in the long fiber (the embryonic fiber of Krause) where the medullated nerve enters. Kölliker (1889) thought their diameter varied from 3 to 15μ. Cajal (1888) showed no striations at the elevation of the medullated ending. Huber and de Witt (1898) pictured the same type of medullated ending but showed striations in the region of the ending itself, which they believed to be epilemmal. Dogiel's description differed in no way from that of Huber and de Witt; like these workers he found that the medullated fibers leave their myelin and undergo frequent branching. None of these authors mentioned Cajal's description of the frog in which he said that a typical motor ending was found on the intrafusal fiber, at one side or sometimes on both sides of the sensory ending. This was substantiated also by Sihler (1900).

The writer finds that the ending described by the previous authors is indeed



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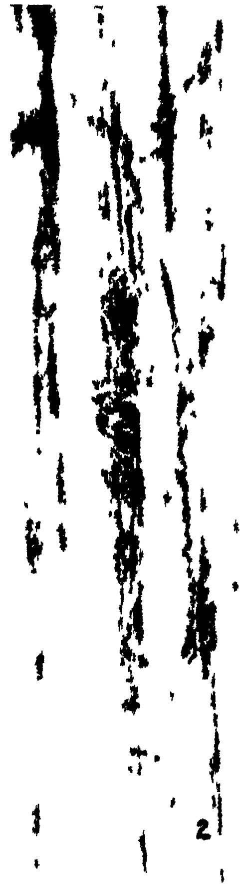

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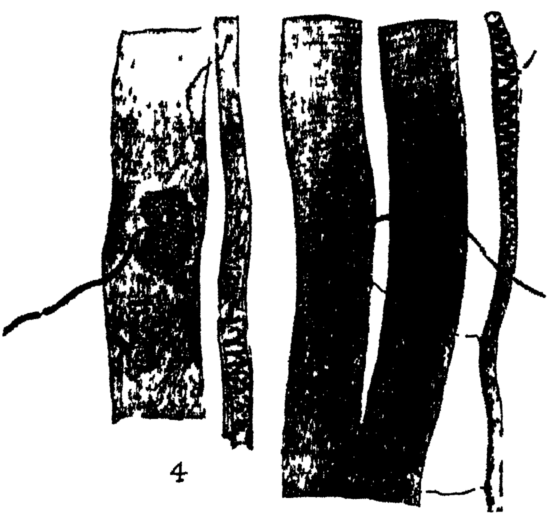

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FIG 1. Muscle spindle of the python, showing the ending of the medullated (thick) fiber, thought to be somatic sensory, and the non-medullated (thin) which Kulchitsky interpreted as sympathetic. Kulchitsky, 1924, pl iv, fig 11.

FIG 2. Normal muscle spindle, stained with methylene blue, taken from the right *M. pectoralis abdominalis* of the frog (No 171). The bulb-like processes are expansions of the axis cylinder of the somatic sensory fiber.

FIG 3 Muscle spindle, stained with methylene blue, taken from the left *M. pectoralis abdominalis* of frog

sensory, because it disappears when the dorsal root ganglion is destroyed, as may be seen on subsequent examination of the sartorius with methylene blue (see Plate 1, figs. 2 and 3). Moreover, besides this ending there is another arising from a non-medullated nerve and appearing to fuse with it. And frequently the route of entry of such a nerve is the connective tissue sheath of a small blood vessel. The non-medullated fiber disappears when the abdominal sympathetic chain is removed. Peculiar as it may seem, when either nerve is destroyed, the clear picture of the morphology of the ending itself is disturbed, although the fibers of the other nerve entering the end organ are intact. A medullated motor end plate was never found on the spindle fiber. The writer, therefore, was unable to substantiate the finding of Cajal and Sihler, although the sartorius and *pectoralis abdominalis* of some two hundred frogs were studied.

It is interesting that Kulchitsky (1924) did not mention spindles in his study of nerve endings in frog muscle although he described at length what he called sensory endings. The writer found in the initial stages of this investigation leaf-like endings similar to his description, but later, when the technique was perfected, they were seen to be the knob-like projections of the sensory innervation of the spindle. The complete innervation of the spindle is so difficult of preservation, that the preparation must be studied within a short time, otherwise its brilliancy is lost. That is probably the reason why the earlier workers failed to find the sympathetic ending. At present the writer has no explanation for failure to corroborate the motor innervation by myelinated nerves as described by Cajal and Sihler.

The muscle spindles of snakes and lizards consist of only one intrafusal fiber, while those of the vastus muscles of the tortoise may contain as many as two to eight (Huber and de Witt). At the sensory nerve eminence many nuclei are found, but there is no interruption in the cross striation. There is no proof in the literature on the spindles of reptiles that the so-called sensory termination is such in reality, for the dorsal root distal to the spinal ganglion has not been cut nor has the ganglion itself been destroyed. Besides this "sensory" innervation, Ranvier (1878) pictured another which he interpreted also as sensory, lying outside the connective tissue capsule. This second ending was first considered by Cajal (1888) and Kerschner (1888) as motor. Later this was believed to be demonstrated by the morphological studies of Sihler (1900), Cipollone (1898) and Perroncito (1901 and 1902, Plate 1, fig. 4), although Giacomini (1898) thought that both might be sensory. By the Loewot-Ruffini modification of gold chloride technique, Perroncito (1901) demonstrated a spiral ending about the central point of the spindle, while beyond that area, the intrafusal fiber received a non-myelinated ending, a branch from a medullated fiber. The termination of the other twig made a typical motor end plate upon striated muscle. Sometimes this second ending took its origin from the medullated motor fiber immediately proximal to the motor plate itself. Such a definite appearance of a divided axis cylinder would point to the fact that the second ending on the intrafusal fiber was motor. This ending, although it may have the appearance of a plaque (Kerschner, 1892), may also look like the *terminaisons en grappe* of Tschiriew (1879) (see Sihler, 1896). Nevertheless, Giacomini (1898) considered it to be sensory because of its morphology. Huber and de Witt (1898), however, although they

pictured these endings as epilemmal, regarded them as originating from a non-medullated fiber and described nothing which resembled Perroncito's findings. Besides this non-medullated motor plaque Perroncito (1902) using the gold chloride technique pictured fine non-medullated fibers twisting about the sensory innervation of the spindle. In 1924 Kulchitsky (Plate 1, fig. 1) using methylene blue technique described in the python the single intrafusal fibers of the spindle, innervated by a non-medullated nerve fiber. This fiber he believed to be sympathetic and the ending from the medullated fiber to be somatic sensory. He worked with teased specimens and fixed with a combined ammonium molybdate and picrate solution. At no time did he report finding the "sympathetic" innervation arising as a branch from the somatic motor innervation of the skeletal musculature. Perroncito, Huber and de Witt, and Kulchitsky all agree in the fact that this fiber near its point of entrance into the spindle is non-medullated; the first two describe it as an ending similar in morphology to the motor end plate, while Kulchitsky with Tschiriew called it a grape-like termination and Bremer (1883), umbiliform. No one has found the very fine non-medullated fibers described by Perroncito in his last paper.

If Perroncito is correct, we find an interesting difference in the motor innervation of the intrafusal fibers of reptiles and amphibians. The former are innervated by a somatic fiber and the latter by a sympathetic. If, however, Kulchitsky's guess is correct, their motor innervations are from the same system. It is difficult to discount such a definite finding as Perroncito presents. Also if Perroncito is correct it is more difficult to understand Sherrington's (1894) finding that the fiber did not show any morphological sign of degeneration following section of the ventral roots. It must also be remembered that the intrafusal fiber of reptiles is very similar to red muscle and is regarded by Sherrington as red in higher mammals. Under these circumstances two types of muscle according to Perroncito would be innervated by the same somatic fiber. This discrepancy may be due to fact, the muscle used for study, the difference in technique, or the particular animal used. Until it is repeated with some accompanying degeneration studies, even the simple anatomical relationship may not be known.

In birds the number of intrafusal fibers varies from two to six in the spindles (Huber and de Witt for the pigeon) within the same muscle. The cross striations of the intrafusal fiber are in evidence even at the nerve eminence (Cipollone, 1897) although less marked than at either end of the muscle. The medullated or sensory fiber enters the sheath of Henle and is distributed over the intrafusal fiber in a manner resembling the description for reptiles. Accompanying it is a non-medullated fiber ending in what Giacomini (1898) called *terminaisons en grappe*, Cipollone (1897) a motor plaque, while Huber and de Witt (1898) do not appear to have seen the fiber in question, although they found a non-medullated fiber within the capsule. They called it a branch of the sympathetic but did not assign any function in relation to the muscle spindle fiber itself. If this nerve were proved to arise from the sympathetic motor cells, and its function varied a little from that found in mammals, there might be a possible morphological basis in the claims of Hunter and Royle for the loss of tone following removal of the sympathetic in the wing of chickens and sea gulls. At present, however, almost nothing definite is known about the innerva-

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Fig. 5. Neuro-muscular spindles from adult cat, showing a plate-like ending, similar to the *terminaisons en grappe*, the central primary spiral and the secondary flower-like ending of Ruffini. Taken from Plate ii, fig. 1, 1898.

Fig. 6 Methylene blue preparation of a muscle spindle from the abdominal muscles of the rabbit, showing the spiral ending of Ruffini and the *terminaisons en grappe* from a non-medullated fiber. From Dogiel, 1902, Taf. II, fig. 14, iv, a.

Fig. 8. Muscle spindle from the *M interosseus digiti* in the cat, stained by the Bielschowsky silver impregnation technique. The degenerated ending is that of C_7. The intact ending arose from T_1. From Agduhr, 1919, fig. 6.

tion of the muscle spindle in birds. It is always possible that a slight difference in morphology may exist and if so, a modification of function might accompany it.

The muscle spindles of mammals are rather isolated organs lying generally in the connective tissue septa between the small fascicles of skeletal muscle fibers. From three to six intrafusal fibers are enclosed in a thick connective tissue capsule (Huber and de Witt, 1898). The capsule contains a blood supply of its own. The intrafusal fibers are surrounded by the periaxial lymph space which Sherrington was able to inject through the lymphatic system. Sympathetic nerves are seen entering it, to do service on the vessels (Huber and de Witt). The spindles vary greatly in length and diameter, according to their age, the particular animal studied, and the muscle in which they are found. Baum (1899) gives for adult man 2 to 10 mm. in length, 0.08 to 0.25 mm. in width; Sherrington (1894) for the cat and ape, 0.75 to 4 mm. and 0.080 to 0.25 mm.; and Batten (1897) for the dog, 3 to 4 mm. for their length and 0.16 mm. for width. The fibers themselves in adult man are about 0.0135 mm. in width as compared with ordinary muscle fibers of 0.0315 mm. (Christomanos and Strössner, 1891). In the mammals studied by Huber and de Witt (1898) spindles were found with areas of nerve distribution varying from one to four. The former were most numerous in the guinea-pig and rat, while the latter were found more usually in the larger laboratory mammals, the dog, cat and rabbit.

Generally speaking, the spindles are more numerous in muscles of the limbs than in those of the trunk, the head or the neck. Onanoff (1890) found them very abundant in the intrinsic muscles of the hand, the flexors of the fingers and the quadriceps femoris. It will be remembered that Huber and de Witt studied the intrinsic plantar muscles of the dog. They are more numerous in the muscles of the thorax than in those of the abdomen. Fraenkel (1878) found them particularly numerous in the thenar eminence in man. In certain muscles, however, Sherrington (1897) says that they are entirely lacking, namely, the orbital eye muscles, the intrinsic muscles of the larynx, the intrinsic muscles of the tongue and the diaphragm. On the contrary, Sutton (1918) was able to demonstrate the neuro-muscular spindle in the extrinsic eye muscles of the pig by following the development of nerve and muscle contacts Pilliet (1890) and Langworthy (1924) have found them in the intrinsic muscles of the tongue in the cat. Cipollone (1897) has not found them in the muscles of the face in the rabbit, nor has O. Cushing Smith (1926, private communication) found them in the facial muscles of the fetal pig, the cat, the guinea-pig or the rat. Cavalié (1902) has not found them in the cremasteric muscle. Baum (1899) did not see them in the muscles of the external ear, in the *M. laryngo-pharyngeus*, the two bellies of the digastric, the stylo-hyoid, or in the muscles ischio-cavernosus and the bulbo-cavernosus. Cipollone (1897) has found them in the external pterygoid and the masseter muscles in the rabbit, while Cuajunco (1926) has demonstrated them in the latter muscle of the fetal pig.

The sensory terminations on the muscle spindle of mammals were seen for the first time by Kerschner (1888) in man. The myelinated fiber entered the capsule, lost its myelin sheath and wound itself about the intrafusal fiber. In the next year Koelliker demonstrated a spiral-like termination. But the best morphological work was that of Ruffini (1892) upon the cat (Plate 2, fig. 5), with a few accessory

studies upon the spindles in man. Using the gold chloride technique he described three different endings, primary terminations or annular spiral, secondary terminations in the form of flowers, and motor terminations resembling motor end plates. The spiral endings of Ruffini are considered by Huber and de Witt as the most typical. They were also described again by Kerschner (1892).

The *terminaisons en forme de fleur* of Ruffini, according to Kerschner and Huber and de Witt are terminal endings of the spirals or their branches, and do not belong in a separate category. In the rat, guinea-pig and rabbit, these spiral endings are not as apparent as they are in the cat, dog and man. Dogiel (1902) working with spindles from the *M. transversus abdominalis* of the rabbit described spiral endings which arise from heavily medullated fibers and grape-like terminations from thinly myelinated fibers. Ruffini thought the primary ending had a heavier medullated sheath. Huber and de Witt, however, described the secondary sensory endings as branches from terminal non-medullated continuations of the spindle nerve which have a zigzag course in an intrafusal fiber without forming a spiral. Both Kerschner and Ruffini have studied the spindles in man and say that the annulo-spiral endings are not there. The termination is compact, and, from their description, somewhat resembles that found in the rabbit.

Kerschner and Ruffini described what they thought was a motor ending. It was probably the same as Dogiel's *terminaison en grappe* (Plate 2, fig. 6), which he believed to be motor. Huber and de Witt were inclined to agree with Kerschner, that some at least of the intrafusal fibers have motor endings. They showed some small plaques which were similar to the pictures of the other three workers.

In rare cases Huber and de Witt said that they found sympathetic nerve fibers in the capsule of the spindle. They believed them to be vaso-motor fibers for the blood-vessels of the spindle muscle and to have nothing whatever to do with innervating the intrafusal fiber itself. Dogiel also saw such fibers and thought that they belonged to the sympathetic innervation of the blood vessels.

These endings described as motor, the *terminaison en grappe* of Tschiriew (1879) at first were thought by him to be sensory; later, although he found them upon fibers with a well developed motor end plate, he continued to interpret them as embryonic forms of motor plaques. Huber (1899) found them upon the extrinsic muscles of the eye of the rabbit. Because there were other typical motor endings, because they formed no Doyère's elevation, were extra-sarcolemmic, were not found in the *retractor bulbi*, were more numerous in the anterior third than the middle third of the muscle, and because no other sensory endings were found in these muscles, he thought them to be sensory. The last reason for believing them sensory vanishes if Sutton's (1915) description of the spindle in the pig proves to be more than a particularization. In the same year (1899) and a year earlier, Sherrington studied the question of the sensory innervation of the eye muscles in the cat and monkey. He reported only peculiar branching of nerves about the tendons, or at the tendon end of the muscles; these nerve branches were undisturbed by section of the ophthalmic division of the trigeminus and were only destroyed by cutting the motor nerve to the eye muscles close to the brain. Elliot Smith (1926) in a discussion at the proceedings of the Section of Neurology, said that Woollard had found such an ending in the eye muscles of the cat and

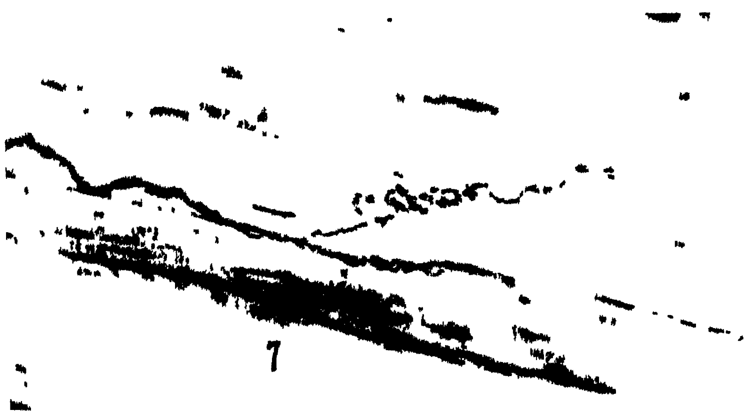

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FIG. 7 *Terminaisons en grappe* stained with methylene blue, found in the *M. pectoralis abdominalis* in the frog. These endings are epilemmal.

FIG. 9 Normal motor end plate on a muscle fiber of the cat's *M. obliquus superior* seen "in profile." The neurofibrilar network ends in the periterminal network, which Boeke believes to be the morphological framework of Langley's neuromuscular junction. Bielschowsky silver technique. From Boeke, 1921, fig. 7.

rabbit. Latham (1924) studied muscles from the limb, the intercostals, the extrinsic (*levator palpebrae*), and the intrinsic muscles of the eye of the fowl, the sea gull and goat. He came to the conclusion that the slender muscle fibers were provided with endings which resembled the *terminaisons en grappe* of Kulchitsky's (1924) description for the small muscles of the python. However, in reptiles (Perroncito, 1902; Kulchitsky, 1924) and in amphibians such as the frog (Plate 3, fig. 7) these terminations or the umbiliform endings of Bremer (1883) are found, especially in the tongue, and in such muscles as the *pectoralis abdominalis*, and the submaxillaris of the frog (Hines, 1926). Landauer (1892) found that they disappeared in the frog when the anterior roots were cut. Although it is not possible to reason from morphology as to whether the ending is sensory or motor, it is not beyond possibility that the *terminaisons en grappe* are sensory in the eye muscles and motor in the spindles and wherever they are found upon skeletal muscle fibers. Moreover, in the frog they do not necessarily appear only in connection with the small fibers, nor do they take the place of a well defined motor end plate as Kulchitsky described for the python (1924), but did not mention for the frog (1924).

In mammals, besides these peculiar endings which are believed by certain authors to be sensory, there are terminal interstitial ones in the intercostal muscles of the dog (Dogiel, 1903) and unencapsulated endings in the abdominal muscles of the rabbit (Dogiel, 1902). Sherrington (1897) said that Pacinian corpuscles occur in the intrinsic muscles of the larynx. Horsley has found them in the gastrocnemius muscle of the cat. Timofejew (1902) has described them in the diaphragm of the guinea-pig and rabbit. Krause (1876) saw them in the flexors of the digits in the sheep. Rauber (1882) found them on the surface of the pectoral muscles of birds. Although it is not absolutely true, nevertheless we may say in general that in those muscles where spindles are not present some other type of ending may be found which investigators believe to be responsible for the afferent impulses leaving the muscles and which probably allows for a better peripheral control of such organs by the central nervous system.

Now, what proof have we of the origin of fibers innervating the muscle spindle in mammals?

Sherrington (1894) cut the ventral roots and the dorsal roots between the spinal cord and the dorsal root ganglion in the cat and monkey. He then obtained a degeneration of the motor fibers originating from the cord, with the sensory nerve intact, but incapable of function. Under that condition the heavily medullated fiber to the muscle spindle appeared normal, 30 to 190 days after the operation. In the cat he cut the sciatic nerve and killed the animal four months later. All the muscles were atrophied except the intrafusal fibers of the spindle which remained intact in spite of the fact that he could distinguish no nerve fibers. He concluded that the intrafusal muscle fibers were not dependent upon the ordinary motor nerves for their maintenance. Nevertheless, his results suggest that the sympathetic, which remained in both instances, was reponsible for the integrity of the intrafusal fiber. Onanoff (1890) attempted to destroy the spinal ganglion, but did not feel sure that the destruction had not injured the ventral root also. In this experiment he found sometimes a few nerve fibers of small calibre in the neuromuscular spindle.

Cipollone (1898) compressed the ab-

dominal aorta temporarily in the rabbit and produced a necrosis of the grey matter in the cord with a subsequent paraplegia, flaccid in type. When he examined the spindles four to ten days later, he found the large medullated fibers intact but the finely medullated fibers and their plate-like terminations on the intrafusal fibers degenerated. If this be true, the plaque is motor, that is, its cell body lies in the ventral horn of the cord, but does not control the nutrition of the spindle. However, the rationale of the experiment is not sufficiently clear cut to be decisive.

Morpurgo (1897) found that exercise in no way modified the size of the individual intrafusal fiber although he found a marked hypertrophy of the skeletal muscle itself. If these nerves are motor they do not affect the intrafusal fiber as do the motor nerves to ordinary skeletal muscle fibers.

Tello (1907) observed that after section of the nerve, the two forms of nerve terminations in the fascicle of Weismann—that is, the termination of the fascicle of Kühne and the motor plaque,—degenerated at the same time, but not with the same rapidity. In preparations 18 hours after section, where the plaques were found in the first phase of degeneration, the fascicle had reached the third or fourth phase. But this does not adequately answer the question of their several functions, although it demonstrates that they are not alike physiologically any more than they are morphologically.

In the same research in which Agduhr (1919a) reported the plurisegmental innervation of skeletal muscle, he presented a similar study upon the muscle spindle. In the cat he cut, in the immediate neighborhood of the *foramina intervertebralia*, the 7th cervical nerve 58 hours, and the 8th cervical 144 hours before death. Afterwards he checked by autopsy and stained with the Bielchowsky silver impregnation method. In the *M. interosseus digiti II* of the anterior extremity, he showed one part of the sensory ending as completely degenerated, C_7, and another as completely intact, Th_1 (Plate 2, fig. 8). There was a slender non-medullated fiber lying in the connective tissue capsule, which he believed to be sympathetic in origin. He thought that the ending upon the intrafusal fiber was sensory because it lay near the middle of the spindle organ and was epilemmal. Furthermore, theoretically, this technique should show a neurofibrillar structure if the ending were motor. Besides these innervated by C_7 and Th_1, he found another group of spindles innervated by C_8 and Th_1. In no case did he find one innervated trisegmentally. The extensor muscle of the forearm contained a smaller number of plurisegmentally innervated spindles than the antibrachial flexor muscles of the same animal.

In amphibians (the frog), then, the mass of data indicates that the motor innervation is sympathetic, that is, its cell body lies in the abdominal chain. In the work previous to Kulchitsky's (1924), leaving out that of Huber and de Witt (1898), the spindle was described as innervated by a non-medullated fiber, a branch of a medullated fiber. The authors mentioned do not commit themselves as to the origin of the non-medullated fiber. Kulchitsky, however, did say definitely that he believed it to be sympathetic. In birds we have nothing particularly conclusive. In mammals, the work of Onanoff and Cipollone suggests that the ending is somatic motor, while that of Tello and Agduhr shows definitely that it is somatic, but does not distinguish beyond doubt the motor origin of the finer medullated fibers.

And yet this nerve fiber must have been destroyed in Sherrington's (1894) study in which he reported a normal intrafusal fiber after the spindle was theoretically stripped of all its innervation capable of function, except the sympathetic. On the other hand, Agduhr pictures, but does not describe, what appears to be degeneration of the intrafusal fiber after cutting the somatic nerve distal to the ganglia. Functionally, Agduhr's experiments and Sherrington's section of the ventral and dorsal roots are equivalent; but morphologically, in those of the former the cell body of the sensory innervation was removed. The exact relation of the components of the peripheral nerves to the spindle and its contents is yet to be analyzed. The origin of these innervations is important for the further consideration of the part played by the proprioceptive fibers, i.e., the muscle sensory fibers, in the reflexes which maintain that elusive quality of muscle Bayliss pleased to call tone.

THE NERVE ENDINGS ON STRIATED MUSCLE

Doyère (1840) was the first to describe the relation of the end branches of nerves to muscle fibers. He noted that at the point where they came in contact a small hillock was visible, Doyère's eminence. At the base of this eminence a great number of nuclei, a part of the muscle, was noted by Kühne (1862). Later (1887) using for the most part the gold chloride technique, Kühne described the continuation of the connective tissue sheath with the sarcolemma, and the branching of the axis cylinder (*das Geweih*) which appeared to become confluent with the sarcoplasm of the muscle fiber; the sarcoplasm at this point was very granular, and surrounded by large transparent nuclei, (*die Sohle*), the sole. His demonstration by means of cross sections, that this ending was hypolemmal has been substantiated by other methods, such as Huber and de Witt's use of the methylene blue technique or lately by Boeke's use of the Bielchowsky silver impregnation method. Kühne believed that the sole is muscle protoplasm and its nuclei similar to muscle nuclei. Huber and de Witt (1898) found nothing granular in their methylene blue preparation of the rabbit motor end plates and suggested that these granulations may be due to the technique used. Kühne thought that the many branched endings in frog muscle were also hypolemmal, but Krause and Koelliker described them as epilemmal. At the termination there is no great heaping up of sarcoplasm, and only a slight increase in nuclei of the muscle itself. The morphology of this ending is more or less peculiar to each animal group. Indeed many times a particular animal might be identified by the morphology of that ending only. Boeke (1921) with a perfection of the Bielchowsky technique that wins the admiration of all who have attempted to duplicate his preparations, was able to demonstrate that the neurofibrils of the axis cylinder, probably a precipitation product, ramify in the form of a network in the motor end plate. This terminal network (Plate 3, fig. 9) of the axis cylinder may be demonstrated in cross section to be continuous with a similar network in the muscle staining brownish, the "periterminal network." Further, the periterminal network appears to be in protoplasmic continuity with the anisotropic bands of the muscle fibril. In only one case, that of *Amphioxus*, did he find the neurofibrillar structure to be continuous with the myofibrillar. The extremely delicate terminal meshes of this network were continuous with the anisotropic discs of the muscle plates themselves. After a

motor nerve has been cut this neurofibrillar network first swells and then fuses, and after two or three days breaks up and disappears; then the periterminal network follows and the sarcoplasm of the sole appears granular. In regeneration, shortly after the new nerve fiber has pierced the sarcolemma the periterminal network reappears in the neighborhood of the neurofibrils. Later it spreads out. The morphology of this ending appears to be closely related to the integrity of the nerve fiber innervating it.

It was early noticed that the nerve fiber was medullated but lost its myelin sheath in the vicinity of the point where it penetrated the sarcolemma of the muscle. This nerve is the motor nerve, the one which, when stimulated, causes the muscle to contract. The question is: is this fiber ever aided in that innervation by another of the same class or of another class? Bremer (1882) shows in figure 22 a motor end plate of a striated muscle from the linguales of *Lacerta muralis* which received a large medullated fiber and a small unmedullated fiber. In 1901 Perroncito substantiated Ruffini's (1894) finding that in reptiles, the lizard in particular, the medullated fiber is often found dividing into two branches, one medullated, the other, non-medullated. The former innervates a skeletal muscle fiber and the latter, the muscle spindle. And occasionally the non-medullated branch may innervate another striated muscle fiber, sometimes the large clear type and sometimes the small granular variety. Strangely enough this second nerve fiber, Ruffini's ultraterminal fiber, does not terminate in an end organ like the other branch, but in one which resembles rather the *terminaisons en grappe* of Tschiriew's description (Plate 4, fig. 10). Such a situation although many times more complicated may be seen in figure 14 of Bremer (1882), a preparation of the *musculus hyoglossus* of the frog. Bremer (1883) in figure 16 shows a non-medullated nerve coming off as a branch immediately before the motor ramification and innervating a spindle from the muscle of the tail of *Lacerta muralis*. It is possible then that the non-medullated fiber which entered the motor end plate may have been a converted medullated fiber of somatic origin. Indeed, the writer has often observed the same peculiarity in the sartorius of the frog, and has proved these fibers to be of cerebro-spinal origin for they persist long after all the sympathetic fibers upon the vessels have degenerated following complete removal of the abdominal sympathetic chain.

Grabower (1902) found in human muscle non-medullated and medullated fibers in the same sheath of Henle; for the most part they ended independently. The non-medullated fiber was often a continuation of a medullated one. Later Gemilli's (1905) observations tended to establish further that this non-medullated fiber was ultraterminal in the sense of Ruffini and Perroncito. A year later Botezat (1906) described in birds an innervation of skeletal muscle by both types of fibers. He did not think that the heavily myelinated fiber which forms the motor end plate became thin and non-myelinated. In fact the endings of the latter were often seen on the muscle fiber in the vicinity of the motor end plates. This second form of nerve ending in the muscle of birds and higher animals may not necessarily be similar to the form seen in reptiles.

From this work of Botezat we have the tempting suggestion that perhaps there are two types of fibers, having different origins. The first definite suggestion came from the work of Boeke (1909, see Plate 4, fig. 11, this paper). In a study

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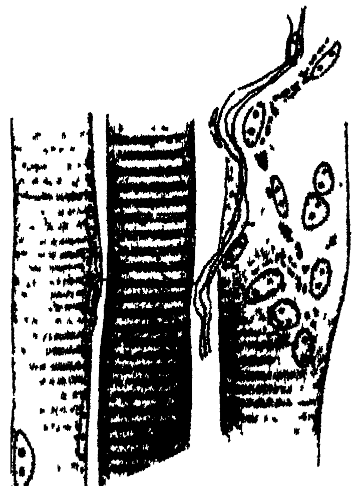

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FIG 10 Motor end plate from the muscle of reptiles Nerve filaments from the motor plaque on the large fiber, which gives rise to a *terminaison en grappe* on a small fiber. From Perroncito, 1902, Pl 2, fig. 11.

FIG. 11 Motor end plate on a muscle fiber from the back muscles of a lizard, showing the ending of the medullated motor fiber and of the accessory non-medullated fiber. Boeke, 1910, Taf. 1, fig. 24.

FIG. 12. Muscle fibers from the eye muscles of the cat. The medullated fiber ending in the plate has degenerated following section of the *N trochlearis*. A non-medullated fiber has persisted. Boeke, 1913, fig. 10.

FIG. 13. Motor endings in the *M. sartorius* of the frog. The same axis cylinder innervates a large and a small muscle fiber. Methylene blue technique.

of the development and morphology of the motor end plate (1910) by the skillful use of a modification of the Bielchowsky technique, he found that after the nerve had penetrated the developing muscle syncytium, a true network of neurofibrils appeared. This was followed by a formation of the periterminal network in what was thought to be muscle tissue. This material did not stain black with silver but was seen as a yellow brown. Then a second motor plate much smaller than the first and also hypolemmal, formed itself in the vicinity of the first and was innervated by an accessory fiber which did not unite with the main medullated fiber. He considered the accessory fiber to be identical with the formation described earlier by Perroncito, Grabower, and Gemelli. In 1910 Botezat published a short note saying that his work on birds substantiated Boeke.

In 1913 Boeke reported that the accessory fiber in reptiles, birds and mammals ended in the neighborhood of the motor end plate. The accessory fiber differed from the main fiber in that it was not covered by Henle's sheath, contained no neurofibrils, did not enter the same plate with the myelinated fiber, but had its own characteristic ending. In *Sturnus vulgaris* I, this fiber was morphologically similar to the one which innervates the smooth muscle of the *M. ciliaris* of the human eye.

Three and four years later he (1916–1917) supplemented this suggestion by experimental degeneration. He cut the oculomotor nerve at its exit from the brain and killed the animal three to four days after. In the study of the ocular muscles the medullated nerve fibers were found to be undergoing degeneration, leaving their non-medullated accessory hypolemmal endings in great clearness (Plate 4, fig. 12). This beautiful experiment was ruined by subsequent inquiry. When three weeks were allowed between the resection and the sacrifice of the animal the greater number of the non-medullated fibers had undergone degeneration also. Boeke suggested that these were cranial autonomic and that they underwent degeneration more slowly than the medullated fibers. Those remaining he interpreted as sympathetic. Then he removed the superior cervical ganglion but this procedure did not cause the complete disappearance of the accessory plates, although he thought them to be fewer in number. There is of course some difficulty in accepting his interpretation that the non-medullated fibers which degenerated in the second experiment were Langley's cranial autonomic system, for these fibers are thought to leave the brain via the third nerve and to form synapses in the ciliary ganglia and should therefore appear intact after resection of the oculomotor nerve near its point of departure from the midbrain. They might rather be the *terminaisons en grappe* fibers described by Huber (1898) for eye muscles.

These inconclusive experimental results were cancelled by two papers published in 1919. Boeke and Dusser de Barrene extirpated four consecutive spinal ganglia (Th 6–9) and cut the corresponding posterior and anterior roots in the cat. Twenty-eight days later the autopsy corroborated their intention. Not a single medullated fiber was intact in the intercostal muscles examined. However, the non-medullated fibers and their end organs remained. Agduhr extirpated the *ganglion stellatum* in two cats and killed them four and six days later. In the six day cat, the remains of degenerated non-medullated nerves could be seen in the interosseus muscles. Further, he performed the converse experiment and cut the posterior roots distal to the spinal

ganglion and the anterior roots in the *foramina intervertebralia*. The animals were killed five to ten days later. All myelinated nerves, both motor and sensory had undergone degeneration. Quite a number of intact non-medullated fibers were found, either in the bundles of degenerated spinal nerves or along the vessels. Such evidence would appear to clinch the original contention of Boeke that the accessory fiber was sympathetic in origin. But it might be well to remember that we do not know whether or not it is sensory or motor, although we do know that the cell body of the fiber under discussion does not lie in the dorsal root ganglion. The extirpation of the *ganglion stellatum* might destroy the sympathetic sensory afferent fiber as well as the motor efferent. At least we know that in two muscles studied the non-medullated fiber innervating skeletal muscle is not somatic.

In 1922 Boeke published a small paper on the innervation of striped muscle in reptiles (Ophidia). He described two endings, the typical motor end plate and a *terminaison en grappe*, which had a sole plate of its own. There was no direct relation of the neurofibrils with the contractile element , but there was a periterminal network whose delicate fibrils could be followed to the anisotropic band of the contractile fibers. He thought that some of these fibers were sympathetic.

The next year Kulchitsky published a paper on the nerve terminations in the python using the gold chloride and the methylene blue dip method. He said that he found the larger, clear fibers innervated by medullated nerves and the small granular fibers by epilemmal unmedullated nerves. Dart (1924) using the same preparations did not see this distinction so clearly. In fact, he figured (Plate 1, fig. 1) three instances of a *terminaison en grappe* and a medullated sole plate lying on the same fiber (taken from ventral mesodermal muscle). There is no way of reconciling these two statements. One observer has made a wrong observation.

However, it was Kulchitsky who startled Hunter's (1925) imagination to take a bold leap. On Latham's meagre finding (with the uncertain gold chloride technique) of a non-medullated collateral arising from a medullated fiber, Hunter dismissed the careful experimental work of Boeke and his collaborators. Latham (1925) himself said that he was unable to stain the nerve terminations to the muscle spindles, although they were present. His technique by his own statement was not adequate. Further, it will be noted that the accessory system with the exception of Bremer's plate was not reported by the earlier workers with the gold chloride and methylene blue technique. It is unfair to say that Boeke's and Agduhr's results cannot be confirmed until a comparison of the two techniques has been made by an experimenter who has mastered both.

Hunter said that Latham examined the muscles of the hind limb of goats, from which the lumbar sympathetic chain had been excised by Royle. "The preparations from the operated side showed in transverse section a number of small muscle fibers which were in marked contrast to those of average size in the same preparation, which were apparently normal." The difficulty is that in Latham's paper on the nerve endings from the goat, fowl and sea gull, he does not make it clear that he is comparing a normal with a sympathectomized muscle. The writer saw the preparations which Hunter brought to Chicago. One or two *terminaisons en grappe* could be easily identified and, as reported, appeared on a muscle fiber small in calibre. But when

Hunter was asked about the source of the preparation in question, no clear cut answer was forthcoming.

It is quite true, as set forth in the discussion of red and white muscle fibers, that the muscles of higher mammals are made up of a mixture of these two types, but it is not known whether or not the white is similar to the large clear fiber and the red, to the small granular one. To recall Hay's work, he found no essential difference in the innervation of a white and red muscle, except the size of the medullary sheaths. Were Hunter's generalization true the red muscles of the rabbit would have to be innervated by the sympathetic system.

It is an interesting observation upon the workings of the human mind to find Kulchitsky's article on the python continually quoted, and his work published later in the same year on the innervation of the muscles of the frog, entirely neglected. In his second paper he does not so much as mention the existence of a muscle spindle in that animal, but describes elaborately endings which he regards as sensory, although the older literature allows no mistake about the existence of spindles in the muscles of the frog. Further, he does not mention the well-known fact that the two types of muscle fibers are characteristic of the frog as well as of the python. Garven (1925) said that in the frog these two kinds of muscle fibers may be innervated by branches from the same axis cylinder (medullated). The writer found has the same with methylene blue technique (Plate 4, fig. 13) and has demonstrated that these fibers degenerate following the cutting of the nerve at its exit from the spinal canal. The sympathetic was left intact.

Garven studied in particular the *panniculus carnosus* of the hedgehog. He thought that in those muscle fibers there were varying degrees of longitudinal striation and varying degrees of content of sarcoplasm and that they could be divided into two definite classes. He reported that all the muscle fibers appeared to be innervated in the same way and Boeke's accessory fibers to be present. The latter reached the endings via capillaries. He found them in frog, lizard and human muscle. These are interesting morphological observations for they support Boeke's data with the gold chloride technique. Garven is undoubtedly correct in his estimate of the innervation of the *panniculus carnosus* in the hedgehog, but this particular case may not resemble the other cases cited.

In O. Cushing Smith's (1926) comparative study of preparations of the facial muscles of the kitten and young guinea-pig with methylene blue technique, it was evident that the simple morphology of the muscle fibers themselves was greatly dissimilar. In the kitten's platysma there were single fibers resembling in morphology the red intrafusal fibers of other mammals, but not lying in connective tissue sheaths. They were innervated by a non-medullated nerve, while the other fibers lying about them had typical motor end plates originating from medullated axis cylinders. In the platysma of the guinea-pig, the morphology of all the fibers seemed to be the same. A rare ending similar to the *terminaisons en grappe* was found.

This is interesting in the light of a personal communication which Cobb (1925) quoted from Bielschowsky, who

> believes that the question of double innervation is still obscure in many ways and needs further study especially from the quantitative point of view. He finds that the end organs described by Boeke are most numerous in the external ocular muscles, less numerous in the facial muscles, and very occasional in the muscles of the extremities.

And yet it was the muscles of the extremities (Agduhr, 1918) and the intercostals (Boeke and Dusser de Barrene, 1919) which were used to prove their existence. To continue, Bielchowsky

> considers it proved that these are sympathetic endings (although certainly Boeke's work on ocular muscles is far from satisfactory in the writer's opinion), saying that the fibers may be recognized by the fact that they are non-medullated throughout their course, whereas the cerebro-spinal fibers only become non-medullated shortly before their junction with the end plate (p. 525).

In résumé, we find that Kulchitsky's work on the python is not supported by Boeke's on snakes, nor by that of Garven on the hedgehog, frog, lizard, and man, nor by that on the frog by Hines (1926). Hunter's separation of innervation of white and red muscle cannot be supported by the inadequate technique of his collaborator, Latham, nor by the work of Hay. In other words, Hunter's generalization does not appear to have an adequate foundation in fact. The whole field calls for reinvestigation with the prevalent techniques in the hands of one who has mastered them and also by one who thinks of nerve endings as organs of activity.

In the light of their uncertain appearance the anatomical facts have been exploited far beyond their factual meaning by the physiologist in search of an anatomical structure upon which to hang his theory of muscle tone.

THE FUNCTION OF THE SYMPATHETIC INNERVATION OF SKELETAL MUSCLE

From the previous discussion it is evident that the muscles selected for study have accessory endings from the sympathetic nervous system. Although there is a definite morphological and physiological difference between the red and white fibers of birds and mammals, and a morphological difference between the clear and granular fibers of lower vertebrates, there is at present no justification for the belief that Kulchitsky's finding of separate innervation of the two types of muscle in the python can be applied indiscriminately to the striated muscle of all vertebrates, nor that the red is equivalent to the granular and the white to the clear. It may be true, but the balance of the data has not settled into the static equilibrium of a proven fact.

Botazzi's (1897) theory that the sarcoplasm of skeletal muscle was responsible for the maintenance of a contracted state, superimposed upon it by the clonic contraction of the myofibrils, was expanded by Mosso (1904) to read that muscle tonus, a characteristic of the sarcoplasm, was maintained by the sympathetic. But what is tonus? Being an anatomist, the writer may not know in this time of specialization, when the right of definition lies only in the province of the specialist, and particularly when observation has found even students of tone to be completely uncertain. Suffice it to say that upon palpation a muscle feels different when all the nerves innervating it and the whole central nervous system of the animal are intact, than when any part of the nervous system related to it is injured. The earliest observation, lost in the obscurity of the past, but demonstrated as a fundamental physiological fact, that after section of its motor nerve the muscle not only loses its contractility but also its feeling of tautness when taken between the fingers remains true. Brondgeest (1860) made the earliest observation known to the writer that this tonus could be destroyed in a muscle by cutting the posterior roots, i.e., the sensory nerves in the region of its motor innervation. The fibers from the posterior roots run with the motor nerve and end

in the muscle spindle (Onanoff, and Sherrington). The maintenance of slight degrees of contraction necessary for the prolonged activity of the antigravity muscles has been thoroughly studied by Sherrington (1915). In that paper he said that reflex postural contraction was characterized by the low degree of tension it usually developed, its maintenance without obvious fatigue, the difficulty of obtaining a resemblance by artificial reflex contraction, the ease with which it is interrupted by reflex inhibition and the reactions of what he calls "lengthening" and "shortening." By the release of lower motor centers in the brain stem from higher control (Weed, 1914; Sherrington, 1898, 1915; Magnus and de Kleijn, 1924) it was found that the "tonicity" of the postural or antigravity muscles was increased beyond that of their antagonists, the flexors,—an experimental procedure, popular with all students of this subject. It is known as decerebrate rigidity. The climax of this differentiation between the two groups of muscles, flexors and extensors, in four footed laboratory animals appears when the phylogenetically old part of the midbrain *nucleus ruber*, cut off from higher centers, can no longer modify impulses from higher motor centers or to the motor cells of the spinal cord. This peculiar condition is modified by the incoming stimuli from the neck muscles and the semicircular canals of the internal ear, and by an intact cerebellum. It is destroyed by cutting the medulla in the region of the eighth cranial nerve (Magnus and de Kleijn, 1924) or by section of the posterior roots (Sherrington, 1897–98).

Thus, physiologically, a dual concept of muscle has arisen. It may contract in response to stimulus or it may maintain a contraction—the contractility and plasticity of skeletal muscle. Sherrington used for illustration of the latter character, the well known fact that the bladder is capable of relaxing and maintaining an almost similar intra-vesicular pressure whether it contains a hundred or two hundred cubic centimeters of fluid. Were the tissue dead, the stretching necessary for the accommodation of the increased amount, read in intra-vesicular pressure, would more closely approximate the increase of fluid. His analogy drawn from smooth muscle, innervated by the autonomic nervous system, together with the work of de Boer and Langelaan has stimulated the other hypothesis, that the sympathetic holds a peculiar power over the plastic quality of tone in skeletal muscle.

To distinguish between these two characteristics, the chemistry of muscle, its electrical response, its action current, its heat of contraction and the action of drugs upon it have been studied. At the present time no resolution of the data presented by workers in these various fields presents itself (see Coman, 1926, and Cobb, 1925).

De Boer (1913, 1914a and b) removed the abdominal sympathetic chain from frogs and cats and reported that the homolateral limbs hung much lower when the animals were held suspended. Even the tail of the cat was bent to the opposite side. Beritoff (1914) reported that there was no change in the tonic reflex activity of the posterior extremities of the frog when the *rami communicantes* of one sympathetic were cut. Dusser de Barrene (1917) found that when the abdominal sympathetic was removed a trifling but plain loss of tone in the muscles followed. It was not an atonia but a hypotonia which in no way resembled that produced by the section of the dorsal roots. It gradually grew less and finally vanished. Cobb's (1918) repetition of de Boer's experiments

offered no support. Van Rijnberk (1918a and b) found that there was no tone in the diaphragm on the side where the phrenic was cut as shown by x-ray nor could he obtain any contraction when the splanchnic was stimulated. Furthermore, he found that decerebrate rigidity always developed on the side where the sympathetic had been cut and that there was no difference in creatinine of decerebrate rigidity after the sympathetic was removed. From this type of experiment, on frogs and cats, it is impossible to conclude that the sympathetic as such has any thing to do with tonicity.

Langelaan's (1915) study of the elasticity and plasticity of muscle under such conditions as increase and decrease of load and its temperature variable bears little or no relation to other studies on tonus. Even his definition that tonus is equivalent to the increase in length of muscle per gram increase of load has no relation to the method of study pursued by other workers. In an atonic muscle this quality has two different elements, an elastic elongation and an after elongation, i.e. tonus is the sum of an elasticity and a plasticity. By means of many measurements and several formulae he concluded that elasticity is a constant and the variation of the tonus is due to plasticity. If we accept his assumptions and definitions and disregard the fact that the muscle is dying gradually, we must admit that his conclusion is the result of inexorable logic. Upon "stimulation of the pretibial muscles by a faradic current and the subsequent contraction of these muscles" there is caused "a considerable increase of tonicity of the *musculus gastrocnemius;* this effect may even persist some seconds after the cessation of the stimulus. The increment of tone is chiefly due to an increase in the plasticity of the muscle." (p. 295). This tonic contraction was not a single contraction but a tetanus. The curves which represent it resemble those of smooth muscle in their tetanic character, stair-case phenomena, slowness of contraction, and slight height. This he said is due to the sarcoplastic part of striped muscle which is innervated by a sympathetic motor cell. The conclusion is obvious, that the plasticity of muscle is dependent upon the sympathetic system. Thus the value of a painstaking study is lost in fantasy and the sympathetic bears away the control of that inexplicable attribute—plastic tone.

In 1922, Langelaan repeated de Boer's experiment and reported a partial but definite loss of tone, thus substantiating his previous observations. In the same year Ducceschi removed the superior cervical ganglion in the rabbit. He reported that there were inclination and deviation of the homolateral ear for many weeks, when the animal crouched at rest. If, however, it was excited both ears were contracted in the same degree. The ears of normal rabbits often may be seen in a position similar to those pictured by him.

Orbeli (1923) used the isolated and therefore bloodless caudal half of a frog to determine whether or not the response of the gastrocnemius muscle to electric stimuli of threshold value applied to the 8th and 9th anterior spinal roots was modified by another thrown into the 7th sympathetic ganglion at intervals. There was no change in the curve until the muscle became fatigued. If the muscle was tetanized for three periods each of five seconds, separated by fifty-five second intervals and then the sympathetic stimulated, the tetanus was held even at a higher level. He thought the sympathetic increased the force. amplitude and speed of development of contraction. He interpreted this effect as trophic. Thus does Pavlov's theory of trophic innerva-

tion gain a new life. Wastl (1925) obtained exactly contradictory results. In the anesthetized cat with intact circulation she stimulated the anterior roots of L 6 and 7 with break shocks at a rate varying from 100 to 220 a minute. At the periods of fatigue of the anterior tibial muscle the lumbar sympathetic was stimulated with faradic current. Six animals showed no change; in three the height of contraction decreased. Following an administration of a small amount of adrenaline a decrease and sometimes a slight increase in height of contraction resulted together with the anticipated brief rise in blood pressure. In the frog, she got no result either with stimulation of sympathetic or by the use of adrenaline. Probably the activity of the sympathetic cannot overcome the fatigue of striated muscle.

Hunter (1924, 1925) and his group of collaborators, with more enthusiasm than critique, have reviewed all aspects of the theory of sympathetic innervation of tone in striated muscle. It is impossible not to be impressed by Royle's results on human patients when the moving pictures of "before" and "after" are seen; just as impossible as it is to understand why the operations performed by the same skillful surgeon in Chicago and Boston did not yield the glowing results of the initial ones made in Sydney. There were three possible differences: first, the Australian patient may have been susceptible of suggestion; second, the skill of the surgeon may have increased; and third, the American patients were not submitted to as long periods of subsequent training. Kanavel, Pollack and Davis in Chicago, without the same type of selection removed the whole of the sympathetic chain in the lumbar or cervical regions and reported no subsequent change with one exception, that of a spastic hemiplegia. In that particular case, the pictures presented at the Chicago Medical Society (Nov., 1924) did show slight improvement, not greater, however, than Franz (1923) reports in his work on reëducation without operation. Carlson thought that the orthopedic surgeons were more optimistic about Royle's results than a physiologist would be, were he examining his own studies on laboratory animals. Crothers (1925) found the cases operated on by Royle in Boston disappointing. The results which followed Royle were not sufficiently encouraging to make this operative procedure advisable. So the hope of surgical intervention in cases of hypertonicity passed.

As for the goat (fig. 6, Hunter, 1925) no one has attempted a repetition of that striking experiment to see whether or not the sympathectomized limb refused to become rigid in the decerebrate animal, and what is more interesting, no one has used Royle's technique in removing the sympathetic influence from the limb of any other animal. It must be remembered that he did not remove the sympathetic chain, nor did he cut the grey *rami communicantes;* he evulsed them, that is he took hold of the ramus with a pair of forceps and pulled it out of the sheath away from its peripheral distribution. It is possible that with the increase in numbers of human operations he performed, the trauma became less, although the form of procedure remained the same. To the writer, this is the only explanation of the divergent results which followed the work of the same man. It may also account for the individuality of the goat. It is strange that they sought for no corroboration upon the common laboratory animals such as the cat or dog. Further, there is no record of the sudden onset of

fatigue in that animal, comparable with that which overtook the sea gull after a flight of an insignificant 100 metres.

In sea gulls and fowls Hunter (1925) performed the following experiment; in the first group he cut the sympathetic chain cephalad of the first thoracic segment; in the second, he sectioned the posterior roots of the first thoracic level; and in the third, he cut the posterior roots of the last four cervical levels. In the first, although considerable tone remained, the abduction and dropping of the elbow was apparent, and became more so under light anesthesia. The fixed position of the flexed wing could not be maintained nor could the bird fly attached to a light line on a smoothly running reel without marked fatigue. Where both wings were so treated, "after several short flights both wings were drooped and the bird was apparently exhausted, the mouth was widely open and the respiration very rapid." In another instance, "the wing was heavy and dependent as in flaccid paralysis." The result following section of the first thoracic posterior nerve upon the posture of the wing was the same as that of cutting the sympathetic chain.

The third operation removed "the tendency of the wing to take up a flexed position, that is, contractile tone is absent. If the wing is passively flexed it will remain in its new position. It has the properties of a plastic body, enabling it to remain in any position in which it may be placed." However, "where the wing is stretched outwards and released it drops to the side of the bird." In other words it was not completely a plastic body. It had lost the ability to oppose the force of gravity, which Sherrington thought so characteristic of posture. The normal mode of contraction, that is, extension of the wing in flight was lost. It was toneless in Sherrington's sense (Walshe, 1925). Walshe (see Adrian, 1926) examined one of the birds on which Hunter had operated. Not only did he think "that plastic tone" as defined by Hunter was absent, but "in addition, the wing was wholly flaccid in passive movement and showed no trace of tonic activity of any kind."

Now, if the first two operations give the same results, Hunter's hypothesis of plastic tone is dependent upon the intactness of the afferent sympathetic arcs. However, there is no proof other than this experiment for the distribution of the visceral afferent, and the distribution of the visceral afferent is used to explain the results. The reasoning is circular. Also, for the anatomical support of this explanation an afferent nerve fiber from the plastic or small muscle fiber is assumed (fig. 2, p. 11)—an assumption which cannot be rooted even in Kulchitsky's work on the python; but rests solely upon the questionable morphological pictures of Latham, that the slender muscle fibers are provided with both hypo- and epilemmal endings. No experimental data were offered. Hunter's theory requires two anatomical facts, not yet in existence, to prove that the afferent part of the reflex arc supports the maintenance of plastic tone. Further, were it true that the afferent and efferent sympathetic arcs connect with the cord via the first thoracic segment and maintain plastic tone, the crucial experiment to demonstrate it was not performed. The dorsal and ventral roots which innervate the skeletal muscle of the wing were not cut simultaneously. In other words, the sympathetic arc was never given complete autonomy. Its isolated function of innervation in birds was not studied.

This report for the hen and sea gull corresponds in no detail with that of Trendelenburg (1906) who divided four to ten posterior roots in the cervical and thoracic

region, thus affecting, according to Hunter's anatomy, both sympathetic and somatic afferents. The normal wing posture was retained and the flight was normal. There was no tonic resistance to passive stretching. When placed in an abnormal posture, it was not corrected. But if the normal wing was also placed in the same abnormal posture, both were returned to the normal. However, after bilateral sections, the resting position of both wings was normal, but superimposed abnormal postures were not corrected and flight became impossible. From this report, "the plastic body," the wing, results from a simple loss of incoming proprioceptive impulses; the motor cells can no longer react to stimuli from that side. It is not plastic when they are stimulated through the afferents of the heterolateral wing.

Kuntz and Kerper (1926) repeated the experiments of Hunter in fowls and pigeons with the same results. However, they severed the sympathetic trunks after section of the posterior roots. The wing no longer tended to remain in the position in which it was placed by the observer, but to hang dependent. These observers did not keep their birds alive 60 days—an experimental condition which is requisite for the defect in the wing posture to become gradually less apparent. It may be possible that the sympathetic exercises a control over posture in birds that is singularly at variance from that which will be described for mammals. Unlike the mammalian forelimb, the wing is covered with feathers and the innervation of their erectile muscles has been destroyed. That loss may mask to some extent a result which would otherwise appear as negligible as from the loss of the sympathetic in other animals. The most suggestive finding is that cutting the posterior root at Th_1 is equivalent to section of the sympathetic chain. It offers a means for determining something about the elusive peripheral afferent visceral ending. The movement of the feathers is one of the few motor responses resulting from stimulation of the cortex in the pigeon (Rogers, 1922). We note that neither observer studied birds under decerebrate rigidity.

Kuntz and Kerper found that under anesthesia a marked difference in the normal and sympathectomized limbs of dogs could be shown. If equal weights were attached to the two hind limbs, the normal was always less fully extended than the operated. Had they cut the dorsal and ventral roots innervating one hind leg, leaving the sympathetic intact, and then demonstrated that under ether, the operated leg and the normal supported an equal weight with the same degree of extension, they would have proven that the elimination of the somatic system by ether was equivalent to experimental resection. If this compared favorably with their previous experiments, the sympathetic would have been shown to subserve some discernible function in striated muscle. They used a modification of Spiegel's (1923) method for obtaining a tonus curve, that is a curve of passive extension of the quadriceps muscle, by what they call the break phenomenon, normally, that muscle offers greater resistance at the beginning of displacement of the limb from a position of rest than when the joint is slightly flexed. It was absent in the leg from which the sympathetic had been removed (from 2 to 112 days). Had they demonstrated by Spiegel's method that an extremity in which the sympathetic alone remained gave a curve similar to that of the intact limb under ether and therefore far removed from the straight line of the denervated limb, they would have approached more

nearly the proof of the sympathetic's responsibility for some part of the tonus of skeletal muscle.

Huggett and Mellanby (1925) found that an intravenous dose of curare, which did not paralyze the sympathetic system, produced complete flaccidity in the rigidity of decerebration, while Combs and Tulgan (1925), contrary to the emphasis placed by Hunter upon the interval between sympathectomy and the production of decerebrate rigidity, reported that immediately after removal of the stellate ganglion from cats, the rigidity of the forelimbs was very much less than that which was found to persist in the hind limbs.

Coman (1926) observed the effect on tonus of the forelimb in cats and dogs from (1) stimulation of sympathetic fibers passing to the limb, (2) section of the ventral roots of the spinal nerves of the thoracic sympathetic, (3) section of the ventral roots of the cerebrospinal nerves forming the brachial plexus. In the first group of experiments Coman said that

> In no animal was there any vasomotor, pilomotor or secretory response in the forelimb resulting from stimulation of roots higher than the fourth thoracic. Moreover, despite observation under the most favorable circumstances to rule out the vestibulo-cervical phenomena of Magnus and de Kleijn, in no case did stimulation of any of the thoraco-lumbar roots result in any detectable tonic effect in the limb musculature.

In the second procedure he found "no tonic, motor, or reflex dissimilarity in the forelegs, either immediately or throughout the largest interval before decerebration." There was no appreciable difference in the two sides in decerebrate rigidity and plastic tonus was not impaired. All the reflexes of posture were equally active. The animals from the third experimental procedure were kept not longer than fourteen days, in order to exclude the factor of muscle wasting.

> Following decerebration, the limb deprived of somatic efferents at no time showed the development of any postural reaction whatever, although normal decerebrate rigidity appeared invariable in the intact limb. Noxious peripheral stimuli, and stimulation of the cut brain stem were equally unproductive of any change in the denervated limb although, as before, the intact limbs reacted normally with augmentation of extensor rigidity. Similarly, passive adjustment of head and neck, while provocative of Magnus-de Kleijn phenomena in the intact foreleg, caused no reaction in the operated leg . . . . Passive flexion or hyper-extension of the operated leg resulted in one of the 'shortening' or 'lengthening' reactions of Sherrington. Plastic tone in the sense of Langelaan was not seen at any time in the de-efferented limb.

In these carefully controlled experiments, no proof is available of a relation between the sympathetic nervous system and either the development or maintenance of postural tonus in striated muscle.

Tower (1926) carried out a series of experiments on dogs in which the stellate ganglion was removed upon one side and the operation without removal performed on the other side. The normal activity of the animals in question was studied, some of them being kept ten months after sympathectomy. They were run (in a motor driven tread mill) for as many as fifteen miles, without great difference in fatigue of the two front limbs, "in fact the greater the fatigue the more alike was the behavior of the two limbs. The differences present at the end of the third mile were lost by the ninth and twelfth." They were studied not only in the decerebrate rigidity preparations of Sherrington and of Davis, but also under such conditions as the hypertonicity of parathyroid tetany and strychnine spasms. "After moderate muscular work, in strychnine poisoning, and in

parathyroid tetany, a tendency for the exhibition of greater tone in the sympathectomized limb was found." There was sufficient evidence of "a quantitative relationship between blood flow and tone to be very suggestive that the circulation through the limb is one of the factors conditioning the tone of the limb." Certainly, the test for fatigue was much more severe in these experiments than in those reported by Hunter on birds.

The evidence presented shifts the balance of responsibility for tone away from the sympathetic. Its removal does not affect the development of decerebrate rigidity, nor modify the reflexes governing posture, nor in the most strenuous tests in mammals does it shorten the time of development of fatigue. At present, in spite of Orbeli's deduction there is no proof of its trophic influence. But there it is, innervating striated muscle. Further, its participation in the muscle spindles of mammals, although suggested by Agduhr, has not been proven except in the innervation of the capsule. Of the part it plays on the intrafusal fibers of birds, nothing is known. There has been no experimental work that proves Kulchitsky's exclusive sympathetic motor innervation of the spindle of reptiles. No other worker has reported a similar finding in that group of vertebrates. The proof of difference between the innervation of red and white muscle fibers in birds and mammals awaits more adequate data for the confirmation of Hunter and Latham. Such a variation in innervation either escaped Boeke and Agduhr, careful observers that they were, or they were unaware of the necessity of making the observation. Of course, this does not prove its nonexistence. The sympathetic, then, is found in some skeletal muscles at least, without anything assigned for it to do. Just how much it participates in the innervation of striated muscles, their contained spindles or other sensory endings, just how that innervation varies from one type of muscle to another and from one animal phylum to another is not definitely known. We are at a greater loss than Mosso and Botazzi to explain its appearance at all, for their supposition, although it has stimulated more observations and theories than the writer has reported, remains one of those theories which has released the biologist's imagination and in the end fails of adequate proof. The same may be said of the Hunter and Royle generalization, magnificent in conception, impossible of proof, and yet the work which it initiated, although it cries aloud for the most part "untrue," is its inevitable result. Perhaps, this review will point out the inconsistencies in our knowledge concerning nerves and muscle in such a manner that work will not be slow in forthcoming to reconcile them. Nevertheless, we must thank the four workers just mentioned for the stimulus of their mistakes, born of insufficient thought and inadequate data, but making an appeal to the imagination which is of major importance. If the reader wishes a poetic definition of tonus, let him read that of Cobb (1925) in the last paragraph of his review. It is full of rhythm and cadence. Also it holds all that we know how to express at this time of that subtle and characteristic quality of normal muscle, tonus. The writer has found no scientifically limiting definition, nothing for instance which matches the physicist's circumscribed concept of force or mass. And until then we see that which is true of tonus through a glass darkly.

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ANIMAL LIFE IN HOT SPRINGS

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SO CLOSELY does the tangled web of life spread over land and sea that it is well-nigh impossible to pick a spot not peopled by animals and plants. Nevertheless, the distribution of any species is determined by the interaction of a series of factors. For the purposes of analysis, we may regard these more or less naïvely as independent and capable of exact statement. Most positive in their action are the limitations set by such physical barriers as oceans and mountain ranges in determining boundaries beyond which most animals and plants cannot pass except under exceptional circumstances. Moreover, such barriers have generally persisted over long periods of time and within the areas thus circumscribed there have arisen characteristic faunas and floras that are quite distinct one from another. On account of a gradual increase in the extent and efficacy of some of these barriers during geological time and an almost uninterrupted action of others over long periods, it follows in a broad way that species are most clearly restricted, genera less so, families still less, and that larger groups tend to be more cosmopolitan. Such a very general statement is by no means accurate in detail since the age of the several groups, their ability to migrate and many other circumstances tend to upset such a simple arrangement. The action of ocean barriers is clearly seen in the faunas of oceanic islands or of large isolated land masses like Australia and Madagascar. Mountain ranges form much less efficient means of herding animals and plants together and their action is in part dependent upon the fact that they interpose a strip of higher, colder land between two lower areas. On the other hand they frequently produce great differences in rainfall between the lowlands which they transect.

CLIMATIC FACTORS IN DISTRIBUTION

The importance of climatic differences in limiting the distribution of animals and plants is dependent mainly upon two factors which are to some extent independent, upon temperature and humidity, the latter in turn determined roughly by the rainfall. Thus the distinctness of the fauna and flora of temperate North America and tropical Central America is in great part a function of temperature, while that between the middle Atlantic States of the same continent (moist transition zone) and the Great Plains (arid transition zone) is due to quite consistent differences in humidity. In neither case do physiographic barriers play a part.

Extremely low temperatures during a considerable part of the year are no deterrent to the successful existence of either plants or animals of many kinds so long as there is a sufficiently long warm season for them to grow and reproduce. Likewise an almost total lack of rainfall and a persistently low relative humidity are equally congenial to the varied assortment of plants and animals that are

adapted to life in deserts, of which there are numerous examples scattered over the globe, each with its quite distinctive fauna and flora.

Compared with the adaptability to intermittently very low temperatures or to continuous dryness, the upper temperature limits compatible with existence, particularly that of animals, are much more rigidly fixed. The maximum warm weather temperatures of cooler climates do not differ greatly from those of the tropics, however greatly the winter minima may drop below the continuous warmth of a tropical climate. Aside from ocean temperatures in the colder seas or currents and in extremely cold climates, the maximum temperatures of the water inhabited by the vast array of animals and plants of aquatic habits vary in comparatively low degree.

FIG. 1. LONE STAR GEYSER, YELLOWSTONE PARK
The cone is of siliceous sinter that has been built up of silica deposited upon growing algae.

There are, however, notable exceptions to the rather uniform temperature conditions which prevail during the season of growth and reproduction in the ordinary aquatic habitat. These are presented by thermal waters or hot springs, the fauna and flora of which shed considerable light upon the temperature requirements of living organisms and their ability to adapt themselves to the higher temperatures and other unusual conditions which prevail in these springs.

OCCURRENCE OF THERMAL SPRINGS

Thermal waters or hot springs occur in many parts of the world, most frequently in places which show signs of volcanic activity. Numerous groups are scattered over Europe; there are famous ones in Iceland, New Zealand and Algeria, and in many countries there are others of minor extent or more poorly known, while there is no doubt that many remain to be discovered or at least accurately described. The temperature of these springs varies greatly and their rate of flow is extremely varied. Some issue violently at intervals from the earth as geysers, emitting superheated water which gives off much steam. Others contain boiling water, but the majority are of lower temperature and these grade down to springs which are hot, warm, tepid, or only to be recognized as of thermal nature by means of a thermometer.

In the United States there are a number of areas with thermal springs. In New York and Virginia there exist a few of very moderate temperature. In Arkansas there are others, but the most extensive

and those exhibiting really high temperatures are in parts of California, Colorado, New Mexico, Utah, Nevada, and finally in Yellowstone Park, Wyoming, which contains the largest and most varied group of hot springs in the world Practically a continuous series with respect to temperature is to be found in Yellowstone Park From the intermittent geysers (fig 1) water at boiling temperature is poured forth, and certain boiling springs or pools are equally hot in places where the water is in active ebullition The outer margins of these pools are cooler and the overflow waters gradually cool as they run off in small streams or spread over the surface of the ground, finally to reach as low a temperature as that of streams or pools of direct meteoric origin Other pools or ponds contain water of more uniform temperature far below the boiling point (fig 2) and often scarcely warmer than ponds of non-thermal origin

FIG 2 BATH LAKE YELLOWSTONE PARK

A warm pool fed by a hot spring near one edge The temperature of the water ranges from about 90° Fahr. to much higher where the spring enters at the far side

BIOLOGICAL PECULIARITIES OF HOT SPRINGS

The biological characteristics of thermal waters depend upon several factors Of these the most obvious is the high temperature of the water The temperature of the medium is a most important consideration and this is the factor which has most generally attracted the attention of biologists Before the beginning of the nineteenth century Saussure (1796) noticed in certain European hot springs that there were both plants and animals living in water at temperatures well above those which obtain in places ordinarily populated by living organisms, and since that time it has become more and more clearly

apparent that the inhabitants of hot springs are in some way endowed with powers of resistance to heat that is fatal to the ordinary run of animals and plants The exact nature of the physiological adjustments of this thermal fauna and flora has so far not been satisfactorily determined, although several theories have been advanced to account for the adaptations which undoubtedly exist

FIG 3 A PORTION OF THE MAMMOTH TERRACES, YELLOWSTONE PARK

These are formed by deposition from water containing dissolved calcium carbonate Algæ occur in these waters at 162° Fahr and below, imparting much color to the deposits

Another common characteristic of thermal waters, particularly of those which emerge from the earth at very high temperatures, is the small amount of dissolved oxygen As a result of this condition the fauna is further handicapped by the dearth of this essential element, except in the case of certain animals, e g , the adults of aquatic beetles or the larvæ of certain Diptera which secure their oxygen not directly from the water, but from the atmosphere above its surface

Thermal water is also commonly impregnated with salts in solution, and the nature of these is naturally very dissimilar in different places, since it is dependent upon the constitution of the rocks with which the heated water has been in contact In the Yellowstone Park springs there are two predominant types, one containing calcium carbonate (fig 3) and the other charged with silica (fig 4) In the former case the water is acid in reaction, due to the presence of much carbon dioxide, and in the latter the silica is dissolved in the presence of sodium carbonate Other salts that are frequently present are sodium sulphate, sodium chloride and gypsum, with occasionally appreciable amounts of arsenical materials The

addition of such substances to the water is naturally an important environmental factor and produces conditions similar to those existing in alkaline lakes or ponds

Hydrogen sulphide is frequently present in considerable quantity, and sulphur dioxide is emitted from certain steam vents After solution in water and oxidation sulphuric acid is produced and causes the charring of wood near such openings

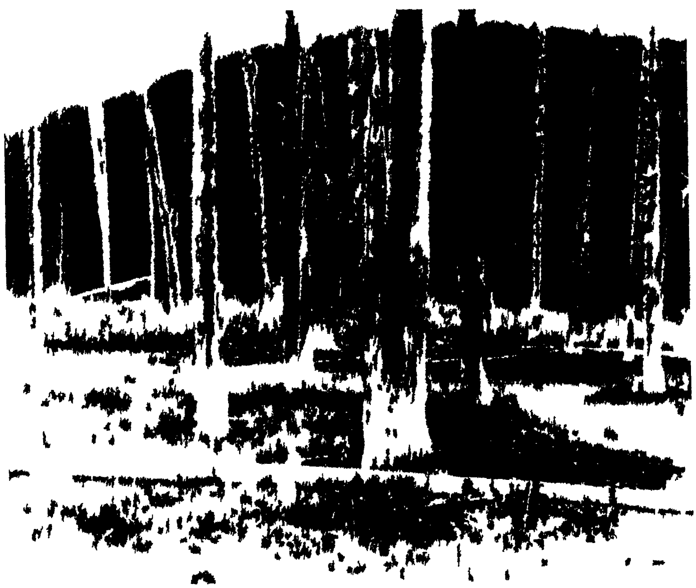

FIG 4 STANDING TREES IN YELLOWSTONE PARK KILLED BY THE OVERFLOW FROM A HOT SPRING CHARGED WITH SILICA

Fallen logs and the stumps of standing trees are silicified by deposition from the water that rises by capillary attraction Many deposits having a similar origin are known from the Tertiary of the Western United States

Occasionally there are also noticeable amounts of finely divided mineral matter present in suspension in pools of tepid water, while in those which are in actual ebullition without much flow of water this liquid may become thick and pasty resulting in mud-geysers or paint-pots '

The ecological peculiarities of the Yellowstone thermal waters are further enhanced by the cold climate of the park, which is located near the 45th parallel of latitude The hot springs are at an altitude of between 6,000 and 7,000 feet, which thus places them within the Hudsonian life-zone In the thermal waters and also in the soil immediately surrounding them much higher temperatures of course prevail throughout the year than are normal for this zone and the rigors of the winter are so mitigated that certain animals and plants have found an opportunity greatly to extend their northern range, irrespective of those that seem to be specially adapted to life in or about the hot springs

THE BIOTA OF HOT SPRINGS

As has long been known, certain plants occur in water of much higher temperature than that at which any forms of animal life are able to exist (fig 5) Several botanists (Davis, 97, Miss Tilden, '98,

Setchell, '03) have made observations of the temperatures at which living plants occur in the thermal waters of Yellowstone Park. Of these Setchell's account is the most complete and embodies a long series of observations on springs of different types. He found in the calcareous springs that chlorophyll bearing algæ occur regularly in water at 60°–63°C. (140°–146° Fahr.) and that forms destitute of chlorophyll extend into still hotter (194° Fahr.). At high altitudes like that of Yellowstone Park, this is practically the boiling temperature of water.

In the thermal springs of Europe many observations have been made, dating back to those of Saussure, who noted in 1796 the occurrence of plants in the waters at Aix at temperatures of from 35°–46°. As early as 1854 De Laures ('54–'55) determined that higher algæ ("conferves") grew in the thermal waters of Néris at tem-

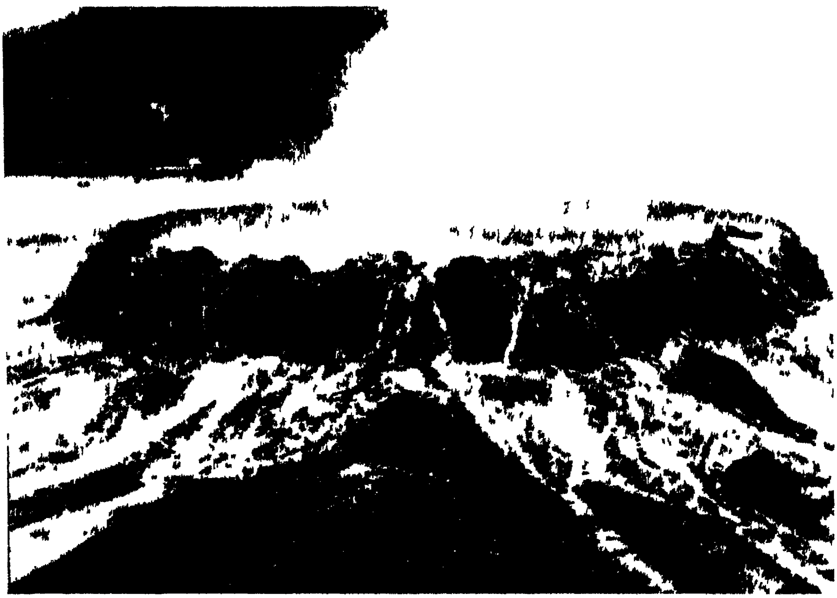

FIG. 5. "PUNCH-BOWL," YELLOWSTONE PARK

A boiling spring which has built up a circular siliceous crater. The overflow water supports growths of algæ which cause a streaking of the sinter deposit with reddish, orange and green.

water of 70°–71°C. (158°–160° Fahr.). These coincide almost exactly with temperatures of 145° and 160° observed by us during the summer of 1923 and with a maximum of 160° reported years ago by Wood ('68) in Owen's Valley, California. In silica-charged waters still higher temperatures are compatible with plant life, as green plants grow in water of 75°–77°C. (167°–171° Fahr.) while those without chlorophyll occur in water as hot as 89°C.

peratures of from 42°–48°C. (107°–119° Fahr.) and he further made the interesting observation that the growth of these plants was augmented during the summer, which he interpreted as due to the influence of light over longer daily periods. In Italy, Hoppe-Seyler ('75) found at Montegrotto near Abano in northeastern Italy algæ growing in water at 50°C. (122° Fahr.) and de Varigny ('93) refers to observations by Martens of *Oscillatoria*

in a hot spring on the Island of Lipari at a temperature of 55°C. (131° Fahr.). A slightly higher temperature of 60°C. (140° Fahr.) is reported for *Oscillatoria* by Schnetzler ('89) at Carlsbad. In the condensed water of steam caves in Ischia Hoppe-Seyler (*l.c.*) found green algæ at a temperature of 64.7°C. (149° Fahr.). In Iceland, several botanists have given accounts of the algæ which occur in the hot springs associated with the well known Iceland geyser region. West ('02) reports filamentous algæ in water at 85°C. (185° Fahr.). These observations accord closely with those made in America.

Concerning hot springs in more distant parts of the world there are few records which appear to be fully trustworthy. In the Himalayas, the eminent botanist Hooker ('54) reported "*Leptothrix*" in the waters of Thibetan hot springs at a temperature as high as 75.5°C. (168° Fahr.). Algæ have been found at Pugha in Thibet at 78.8°C. (173° Fahr.) and Dana noted algæ obtained at 160° Fahr. (72°C.) on the island of Luzon. In South America he speaks of vegetation in hot springs at Las Trincheras in Venezuela occurring in water as hot as 71°C. (160° Fahr.).

In the extensive hot springs at Hammam-Meskoutine in Algeria, Gervais ('49) found algæ in the second tier of basins of the cascade where the water registered 57°C. (135° Fahr.), but the upper series with a temperature of 63°C. (146° Fahr.) was without them.

Some of these records refer to green algæ, and others like the one at Las Trincheras undoubtedly relate to species without chlorophyll. With this in mind, it is evident that they agree closely with what is known of the algæ and other primitive plants in the thermal waters of Yellowstone Park, with the possible exception that no European species without chlorophyll appear to have been reported from such extremely high temperatures as in other parts of the world.

TEMPERATURE REQUIREMENTS OF ANIMALS

The temperature requirements for animals of all kinds are much more exacting than those for the lower plants and will be considered more in detail in a moment. Compared with plants their powers of adjustment to high temperatures are considerably less, and even the most resistant forms of animal life are unable to endure the degree of heat at which certain plants thrive.

Practically all groups of animals that are represented abundantly in fresh water contain a few species known to inhabit thermal waters. These forms thus make up an extremely varied although not by any means a rich fauna, similar in some respects to that of a volcanic island that has been peopled by visitors from the outside world.

From data furnished by experiments on certain marine animals it is evident that those forms which have always lived in the sea where they are never called upon to combat great fluctuations in the temperature of the water are very susceptible to injury from excessive heat. Experiments upon a variety of marine animals like crinoids, actinians, ctenophores, worms, crustaceans, molluscs and fish with respect to the temperatures they can withstand without immediate harm when the medium is slowly heated show that temperatures of 25°–30°C. (77°–86° Fahr.) are the highest that can be borne even for a few hours, although the mollusc, *Murex* (32°), and some actinians (38°) exceed these figures. These critical points apply quite closely to such other marine metazoa as have been examined.

As there are no marine forms occurring in hot springs it is of course impossible to

say what their powers of temperature adjustment might be after acclimatization over long periods, but when transferred from a uniformly cool environment it is evident that they are quite susceptible to heat and that forms like the actinian and snail just mentioned, which must normally be subjected to excess heat in the littoral of the sea, show the greatest resistance. The larvæ of certain marine littoral animals withstand higher temperatures. Some molluscs, annelids, trematodes and crustaceans are frequently killed by exposure at 30°–31°C. (86°–88° Fahr.), while others withstand 37°C. (97° Fahr.). Embryos of the common pond-snail, *Lymnæa*, survive a heating of the medium to 44°C. (110° Fahr.).

On account of the great fluctuations of temperature in all except the largest bodies of fresh water, the animals which inhabit them are periodically subjected to considerably higher temperatures than those encountered by marine forms, and we find that the fresh-water fauna is much better able to withstand extremes of heat. Observations on certain Amphibians by Davenport and Castle ('96) and others show that these animals are unharmed by temporary heating of the medium to about 38°C. (102° Fahr.). In thermal springs the tadpoles of certain tailless batrachians have been found living at temperatures noticeably above this and as these are species known normally to inhabit waters of meteoric origin, it is evident that they have become acclimatized to these higher temperatures by exposure extending over a number of generations. Fishes are more susceptible to heat, although there is evidence that certain forms have been acclimatized in a similar way. Even fresh-water turtles occur in hot springs according to Schmarda ('53), who cites the finding of these animals in Tunis in springs near the ancient Utica at 44°C. (111° Fahr.) and near Lenkoran on the Caspian Sea in sulphurous springs at 40°C. (104° Fahr.). Among invertebrates the molluscs and insects are most abundantly represented in thermal waters and, as indicated in detail later, certain members of these groups extend into water of 40°C. (104° Fahr.) and several degrees higher in a few instances.

ACCLIMATIZATION TO HIGH TEMPERATURES

The range of temperature over which the process of acclimatization may extend is nevertheless very limited and moreover very uniform among quite diverse animals. This is beautifully illustrated by the classic observations of Plateau ('72), who determined experimentally the thermal death point of a number of fresh-water arthropods known to occur in thermal waters as well as in ordinary ponds and streams. When we compare the temperatures at which these animals actually occur in hot springs with the highest temperature that that can be successfully endured by unacclimatized individuals of the same species we find that the possible range of acclimatization although not great is of quite consistent magnitude. This is evident from table 1 compiled from tables given by Plateau.

Practically all of the species listed above show that there has been an adjustment which enables them to live continuously at temperatures higher than those at which they are able to remain alive for more than a few minutes when taken directly from fresh water at ordinary temperature. The differences amount, however, to only a few degrees in each case and we may conclude that the range of temperature adjustment is ordinarily only from one to several degrees centigrade.

The Protozoa are the most resistant of all animals, and rhizopods and flagellates have been found in Italian hot springs at

54.5°C. and 51°C. (130° and 124° Fahr.) respectively by Issel, who also discovered an amoeba, apparently the common *Amœba limax*, in the water at 50°–52°C. (122°–126° Fahr.) and ciliate infusorians at 46°C. (115° Fahr.) ('00, '01, '10).

THE FAUNA OF THE DESERT

The exact relations of terrestrial and aerial animals toward the temperature of the soil and air about them are much more difficult to determine than is the case with aquatic forms. Several reasons for this are self-evident. The specific heat of water is much greater than that of air and soil and the closeness of contact with the soil is so much less than in the case of water that the body heat of cold-blooded animals responds far more quickly and accords very closely with that of the water. The cooling effect of evaporation can also greatly reduce the body heat of non-aquatic animals. Finally, the vast differences between sunlight and shade temperature are in turn modified by the external color of the animals themselves. With such a mass of variable factors, coupled with the fact that most animals may seek the sun or shade at pleasure and may choose between a period of diurnal or one of nocturnal activity, the actual temperatures to which such animals are subjected and the periods of time involved are to be determined only approximately.

TABLE 1

Range of temperature acclimatization

SPECIES	HIGHEST TEMPERATURE AT WHICH UNACCLIMATIZED INDIVIDUALS REMAIN ALIVE	TEMPERATURE AT WHICH INDIVIDUALS HAVE BEEN FOUND IN THERMAL WATERS	LOCATION OF THERMAL SPRINGS
Insects:			
Mosquito larva—*Culex pipiens*	38°C.	40°C.; 39°C.	Néris; Luxeuil
Mayfly nymph—*Cloë diptera* (nymph)	44°(?)	45°	Luxeuil
Water-bugs:			
Notonecta glauca	37.5°	45°	Vichy
Nepa cinerea	43°	45°	Vichy
Water-beetles:			
Agabus bipustulatus	36°	38°	Ems
Hydroporus dorsalis	39°	42°	Loèche-les-Bains
Hydaticus transversalis	38°	39°; 39.2°	Luxeuil; Ems
Hydrous caraboides	38°	40°	Néris
Arachnids:			
Argyroneta aquatica	37°	38°	Ems
Hydrachna cruenta	44.5°	46°	Luxeuil
Crustaceans:			
Asellus aquaticus	38°	42.5°	Loèche-les-Bains
Daphnia sima	32.5°	25°	Luxeuil
Cypris fuscata	35°	34.4°; 36°	Piedmont; Gastein
Cyclops quadricornis	35°	34.4°; 36°	Piedmont; Gastein

In nature the most obvious field for comparison with the aquatic thermal environment is the desert. Desert animals are at times subjected to high temperatures which are quite comparable to those encountered by the inhabitants of hot

springs. Here the most important difference lies in the opportunities enjoyed by the members of the desert fauna to escape the excessive heat (and also the dryness) of the surface of the soil by burrowing beneath it during the warmer parts of the day. According to Buxton ('23) the surface temperature of the soil of the desert may normally reach 122°–140° Fahr. (50°–60°C.) in parts of Palestine, while even of higher readings of 78°–84°C. (173°–184° Fahr.) have been obtained in other desert regions. He also noted the occurrence of certain insects, nymphs of two species of *Mantis*, and adult grasshoppers, actively moving about on the ground where the superficial temperature was 50.8°C. (121° Fahr.) As the opportunities for bodily temperature reduction are very slight in such chitin-encased animals devoid of any special regulatory apparatus for this purpose and possessing only a very scanty supply of water, the conclusion appears inevitable that the temperature of their bodies cannot regularly be far below that of the soil surface. Buxton ('24) has actually taken the bodily temperatures of certain desert insects by means of a minute thermocouple which can be inserted *per rectum* into the body of the insect. By this ingenious device he has been able to determine that the body temperature may approach closely to that of the heated soil, but that it always appears to remain slightly lower. Thus in the black tenebrionid beetle, *Ademsia ulcerosa*, body temperatures of from 36°–39.5°C. were found where the substratum registered 38°–44°C. and in several pale colored insects the body was somewhat cooler in proportion, registering 33.5°–39.5°C. when the surface of the soil was 39.5°–45°C.

It is evident from these and other observations that the temperatures tolerated by desert insects correspond closely to those endured by the inhabitants of hot springs.

THE THERMAL DEATH POINT

Under experimental conditions the effect of certain modifying factors may be eliminated and this has been done to some extent by several entomologists who have determined the reactions to excess heat and thermal death-point of various unacclimatized insects. Cantoni ('72), Bachmetjew ('01), Dewitz ('06) and others have found that the larvæ of various moths and flies will tolerate temperatures of 40°–45°C. for more or less prolonged periods or somewhat higher ones (47°C.) for shorter ones. Most of these experiments place the upper limits of temperature tolerance in the neighborhood of 40°–41°C., or 104°–105° Fahr.

In connection with his studies upon the symbiotic intestinal protozoan fauna of termites, Cleveland ('23; '24) has examined with great care the reactions of both termites and protozoa to high temperatures. He found that the thermal death point of the intestinal protozoa is 36°C. (97° Fahr.) while that of practically all of the species of termites with which he worked was considerably higher. The host termites were entirely unaffected by a 24 hour exposure to 36°C. and were able to withstand without injury exposures of ten minutes to 42°–47°C. (108°–117° Fahr.). He thus regards 48°C. as the thermal death point of the termites, although with longer exposures this would no doubt be lowered to some extent.

The very general agreement of nearly all of the observations relating to the fauna of thermal springs with experimental data secured from other animals of the most diverse sorts shows that the tolerance of all animals to high temperatures coincides within quite narrow limits. These

would appear to range between 40° and 45°C., or 104°–113° Fahr., usually nearer the lower figure, except in the case of marine species, to which as already stated temperatures above 25°–30°C. quickly lead to death. There is also a close agreement between the limits above indicated for non-marine animals and the body temperatures of warm-blooded animals. As the latter are equipped with a thermoregulatory mechanism and are of course not subject to the fluctuations of the medium in which they live we must look for abnormal conditions to determine the upper limits of body-temperature compatible with continued life. Such conditions are furnished by individuals, including those of our own species suffering from acute febrile diseases, where the failure of the regulatory apparatus allows the body temperature to rise. Under such conditions a rise of body temperature of a few degrees above the normal level of 37°–42°C. (99°–108° Fahr.) is fatal to the animal. This is in close agreement with the reactions of the lower animals toward heat, especially when we consider that the homoiothermal animal must be regarded as acclimatized to high temperature; or, in other words, that the warm-blooded vertebrate normally maintains a body temperature very close to the thermal death point.

This uniformity of reaction among the most diverse animals would seem to be due to the fact that high temperatures act directly upon their protoplasm, or at least upon cell metabolism, and this view finds support in the experiments of Vernon ('99) who found in a series of both vertebrates and invertebrates that the voluntary muscles pass into a condition of rigor at temperatures approximating the lethal temperature limit. Unfortunately no satisfactory understanding seems to have been reached concerning the physiology of this process, for upon it must depend any theories relating to the acclimatization of animals to high temperatures. Davenport and Castle ('96) advanced the theory that the increased resistance of organisms acclimatized to heat is due to a partial dehydration of the protoplasm whereby on a purely physical basis, its coagulation point is raised in the temperature scale. This explanation is based partly on the fact that albumen coagulates at higher temperatures as its water content is decreased, and in part on the resistance of the spores of many microörganisms to temperatures far above those that can be withstood by their actively growing stages. That the same condition holds true in encysted or desiccated infusorians and even in minute metazoa like rotifers and tardigrades is also apparently well authenticated. In these animals the amount of exsiccation without loss of vitality is surprisingly large. Even in frogs it may proceed to a point where as much as 41 per cent of the body weight may be lost (Hall, '22) and subsequently regained without ill effects; such an occurrence normally follows the periodic changes of the season in certain Australian desert frogs. Setchell ('03) from his study of the thermal flora is not inclined to accept this view of exsiccation, at least in regard to the thermal algæ. Applied to the thermal fauna this theory would imply a decreased water content in the blood and tissues and it seems probable that their saline content in most invertebrates is actually greater, due to the excess of salts in the medium which pass into the blood and tissues (Frédéricq, '04). That an actual change of constitution such as coagulation in a substance like albumen through heat can apply directly to account for acclimatization in animals is very improbable for the lethal tem-

peratures for animals are very much lower than those for plants.

ORIGIN AND RELATIONSHIPS OF THE THERMAL FAUNA

It is evident that those fresh-water types of animals which are able to adjust themselves to the highly saline water of brackish ponds or of the ocean itself are those which most generally occur in thermal waters. The similarity between these two faunæ and that of the littoral zone of the sea also is very striking and cannot fail to impress any zoologist who cares to examine the thermal fauna in any detail. It may be said that a great majority of the animals which occur in thermal waters have close relatives which live in alkaline, saline or brackish water or even in the sea. As the only similarity between all such situations lies in the considerable amounts of soluble salts in the water, irrespective of their nature, it seems reasonably evident that the fresh-water groups of animals that have developed species adapted to thermal waters have done so through their ability to adjust their metabolism to the increased osmotic pressure of the medium. That the members of a number of small, quite unrelated groups possess this ability to an unusual extent is equally evident. That much variation occurs among animals in this respect is of course well known (*cf.* e.g., Garrey, '05; Sumner, '06), and the cases cited indicate that it is not safe to draw broad conclusions regarding extensive groups of animals from experiments with members of isolated genera or families.

In practically all thermal waters there is undoubtedly a considerable deficiency in dissolved air and a dearth of oxygen compared with meteoric waters, as gases are naturally in great part expelled from the highly heated waters when not under pressure. Thus in the overflow from geysers and in pools rapidly supplied by water from boiling springs the process of cooling to temperatures compatible with animal life takes place quickly and there is little opportunity for atmospheric air to be absorbed. The green thermal algæ growing in such water are a source of oxygen supply but the amounts which they are able to furnish to rapidly moving water must be slight even where they are present in a considerable quantity. In the hottest water non-chlorophyll bearing plants (like the sulphur bacteria, *Beggiatoa*) of course furnish no oxygen and their occurrence indicates the presence of some oxygen in the water when it reaches them.

As already mentioned, many of the animals, e.g., many insects and snails, are not entirely dependent upon the dissolved oxygen as they obtain atmospheric air. Nevertheless some are entirely dependent upon what they extract directly from the water, like the crustacean, *Gammarus*, and the larvæ of the fly, *Chironomus*, and those of water-beetles. In reference to the fauna of fresh-water lakes it has been conclusively shown that the amount of dissolved oxygen, which varies at different depths, is an important factor in determining the distribution of fishes and certain water-breathing invertebrates (Juday, '09; Juday and Wagner, '09). It is interesting to note that at least one type which Juday found to be characteristic of the lower water layers of Wisconsin lakes occurs in what appears to be one of the most anaërobic situations where I have found living animals in the thermal waters of Yellowstone Park. These are the larvæ of *Chironomus*, commonly known as blood-worms on account of the red hæmoglobin pigment which they contain.

The thermal fauna has, as already stated, undoubtedly been derived mainly

from an assemblage of fresh water animals that have found a suitable if not ideal environment in more or less saline waters of abnormally high and uniform temperature. We cannot, however, consider it at all homogeneous either in origin or in constitution. On the basis of our conception of the geological development of the earth we have only to go far enough back in the evolution of life to reach the point when all animals and plants belonged to a "thermal fauna." Just how elaborate and highly differentiated living organisms may have been at the time when all water on the earth was at a considerably higher temperature than at present is by no means to be stated. Our knowledge of fossil animals does not, however, suggest in any way that highly evolved types were present at that time and certainly no one would entertain for a moment the idea that arthropods or molluscs were then in existence. Even if other evidence did not preclude such a possibility it would therefore be fallacious to trace any great part of the present thermal fauna to a primordial one. Schnetzler ('89) would trace some of the highly adapted lower thermal plants like *Oscillaria* and certain diatoms to a primordial flora, an assumption which is far more plausible.

There is no doubt, however, that thermal springs like those now extant have existed in the past, as there remain widespread evidences of their activity. It is well known that many fossil plants owe their preservation to the deposition within their tissues of silica derived from hot waters charged with silica in which they have been immersed or from which they may have imbibed the solution by capillary attraction. The "fossil forests" of tree stumps, logs and bits of wood have originated in this way, and in one instance at least it is evident that deposits of fossil insects are to be attributed to the same source (Cockerell, '15). In the Gurnet Bay deposit on the Isle of Wight there is an accumulation of this sort which includes many insects in addition to numerous molluscs. These were perhaps caught in a mud spring, with heated waters, into which the insects fell, overcome by gaseous emanations.

This Gurnet Bay formation is early Tertiary, probably lower Oligocene and in connection with the present day fauna of thermal springs it is interesting to compare the forms which have been found there. Thus in his account of the insects, Cockerell finds two species of *Ephydra* and *Stratiomyia*, both of them genera known to contain modern species that breed in thermal as well as saline waters. In addition there are winged ants and other Hymenoptera, quite similar to the miscellaneous assortment of insects that fall into hot springs. Certain deposits of silicified wood are much older and the preservation of some Cretaceous and even Jurassic wood is so similar to that now in process of silicification that there can be little doubt that the hot springs which furnished the silica were so like those of the present day that they offered similar opportunities for animal life.

On the basis of these facts it may be stated that very probably there have always been hot springs and that they have presented quite similar conditions for a long time, but that their fauna has had its origin in animals from cool fresh water that have become adapted to life in the higher temperatures and more saline water of thermal springs.

COMPONENTS OF THE THERMAL FAUNA

The present day fauna we may regard either from the standpoint of the temperature and other characteristics of the water or on the basis of the origin of

its several components. Vouk ('23) has grouped the thermal fauna and flora in three divisions in relation to temperature, as follows:

Hypothermophilous Formations, below 15°C. (58° Fahr.).

Mesothermophilous Formations, 15°–30°C. (58°–86° Fahr.).

Euthermophilous Formations, 30°–80°C. (86°–176° Fahr.)

This classification is essentially arbitrary and artificial as it fails to recognize the varying critical temperatures for different types of organisms, although in its gradually rising scale, it necessarily reflects to some extent the progress of adaptation. From what has already been said concerning the temperatures withstood by unacclimatized animals of most kinds it is evident that there is a clearly marked point in the neighborhood of 40°C. (104° Fahr.) which is highly significant as it is the upper limit for all but the most resistant animals. Among plants on the other hand as already mentioned temperatures in the neighborhood of 60°C. (140° Fahr.) are critical as they mark the upper limits for chlorophyll-bearing vegetation.

From the standpoint of origin, Issel ('06) recognized five groups of animals in thermal springs:

1. Animals derived from cold water, usually species which are much more abundant and widespread in various other environments, and consequently with a greater ability to accustom themselves to extreme conditions.

2. Animals that come periodically from the sea or which migrate for short periods into fresh water from the sea.

3. Animals that, although absent in the ordinary waters of the region, occur in that of warmer regions.

4. Animals at present restricted to the thermal waters of a region, but similar to fossil species of much wider distribution in deposits from ordinary water in the same region.

5. Animals which are so far as known apparently restricted to thermal waters.

This classification is based on the probable evolutionary development of thermophily. The most recent accessions to the fauna are placed in the first category, and those types which are undoubtedly the oldest are placed last; the arrangement thus conforms to the probable origin and development of the thermal fauna as we have outlined them above. In many hot spring areas there is no access for animals from the sea, and the distinction between the fourth and fifth category is rather arbitrary. So far as category three is concerned this is an example of the fact that animals requiring moderate winter temperatures extend further toward polar regions wherever local conditions mitigate the rigors of the cold season.

As mentioned on a previous page, the most obvious characteristics of the thermal fauna are its evident origin from that of cooler water and its accession of a preponderance of types that are well represented in brackish or alkaline bodies of water.

INSECTS IN HOT SPRINGS

Many insects occur in hot springs, and these belong to a number of diverse groups. Numerous representatives of several families of aquatic beetles are known from thermal waters, mainly of Europe and the United States. Indeed, the members of this order occur more generally and abundantly in thermal waters than those of any other group of insects, and moreover, there appear to be some species that are restricted to warm springs and able to thrive at somewhat higher temperatures than those generally suited for animal life.

Several years ago in Yellowstone Park the writer collected six species of beetles in water of about 90°–100° Fahr. Of these three have close relatives that occur

FIG. 6. WATER-BEETLE, *Tropisternus californicus*
Both larvæ and adults were taken in pools at 90°–100° Fahr. in Yellowstone Park.

in brackish water. In hot springs in Arizona, Schwarz ('14) reported two species living in water at 110°–115° Fahr., and two of these, *Hydroscapha* and *Bidessus*, are characteristic denizens of European hot springs. In adjacent cooler water (100° Fahr.) there were eight other water beetles, most of which were to be found in the neighborhood in waters of ordinary temperature. In Europe another species of *Hydroscapha* occurs in Italian hot springs at temperatures of 30°–46°C. (86°–115° Fahr.) according to Issel ('01; '10) who found two European species of *Bidessus* at 30°–45°C. (86°–113° Fahr.). From these and numerous other observations on beetles we see that some kinds are adapted to extremely warm water and that all are in general closely related to types that extend into other saline environments.

Among other insects, the Diptera show the most interesting relations to thermal waters. Several families are represented: midges (Chironomidæ), horse-flies (Tabanidæ), soldier flies (Stratiomyiidæ) and Ephydridæ. The midges, which are all truly aquatic in their larval stages, include a number of genera that are exclusively marine, or which are represented by one or several species in the shallow parts of the sea. The larvæ of several species of *Chironomus*, like the vertebrates and in common with a very few other invertebrates, are provided with the respiratory pigment, hæmoglobin. In these larvæ the hæmoglobin is dissolved in the blood, which becomes a brilliant red and has earned for them the name of "blood-worms." Blood-worms occur more or less commonly in mud beneath water, in water-lily roots and in the deep water of lakes, while some other chironomid larvæ occur in sea water even at considerable distances off shore. In Yellowstone Park I found one species (fig. 7) abundant in the mud of a shallow thermal pool at a

FIG. 7. "BLOOD-WORMS," *Chironomus*
These insects develop in mud, in lake water practically devoid of oxygen and in thermal water, sometimes at unusually high temperatures of 120°–124° Fahr.

temperature of 120° Fahr. (49°C.). As early as 1868 similar larvæ were reported by Owen from a Californian hot spring at 124° and more recently several others have found them in other American and European springs.

Leitch ('16) has studied experimentally the rôle of hæmoglobin in *Chironomus* and also in the snail, *Planorbis*, and comes to the conclusion that the function of hæmoglobin in these two animals, and among those invertebrates in general where it occurs, consists in making available, by its power of binding oxygen chemically, a quantity of oxygen sufficient for the needs of the animal at oxygen tensions so low that the necessary amount is not supplied by physical solution. He has shown also that the actual storage capacity for oxygen of the hæmoglobin in the larva of *Chironomus* is sufficient for only a few minutes of anaërobic life Thus hæmoglobin is characteristic of many mud-inhabiting invertebrates (van der Hyde, '22) that live where oxygen is present in only very small amounts. On the basis of Leitch's data we may thus interpret the ability of the larvæ of *Chironomus* to live under more or less completely anaërobic conditions, and we find them in the lower waters of lakes where the presence of oxygen cannot be detected by ordinary means. This is a common occurrence in fresh-water lakes (*cf.* also Immel, '16) and in thermal waters (Ziegelmayer, '24). In the alkaline water of silica-bearing hot springs

FIG. 8. SOLDIER-FLY, *Stratiomyia;* ADULT ABOVE, LARVÆ BELOW

The encrusted larva at the left has been overflowed by very hot water which killed it and deposited a heavy coating of calcareous material upon its body.

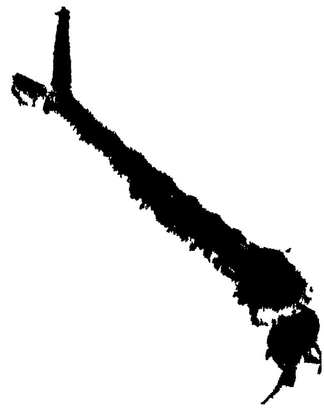

FIG. 9. MOSQUITO LARVA, *Culex tarsalis*, FROM SLIGHTLY WARM THERMAL WATER OF A TURBID POOL. YELLOWSTONE PARK

FIG. 10. CATERPILLAR IN THE PROCESS OF CRUDE FOSSILIZATION BY THE DEPOSIT OF CALCAREOUS MATERIAL ON ITS BODY. THIS UNHAPPY CREATURE FELL INTO WATER OF VERY HIGH TEMPERATURE

there is the added fact that among fishes at least, an increased alkalinity serves in some way to increase the resistance of these animals to a lack of oxygen (Packard, '05) and the same is probably true

Fig. 11. Horse-Fly, *Tabanus punctifer;* Larva at Left

The larva develops in alkaline lakes and in thermal water of moderate temperature. Taken in water at 91° Fahr. in Yellowstone Park.

of *Chironomus* as the hæmoglobin appears to be identical in the two cases.

The larvæ of stratiomyid flies have been found several times in thermal waters both in America and Europe and some are known to occur in the sea. Some belonging to the genus *Stratiomyia* (fig. 8) found by the writer along the edge of a hot streamlet in Yellowstone Park well illustrate the vicissitudes of life in such surroundings. These larvæ dwell in the algæ along the cooler edges of the stream, but when the latter changes its course, as frequently happens when mineral deposits clog its channel, the larvæ may be immersed in water hot enough to kill them. Deposits then cling to them and they become rapidly though somewhat crudely fossilized.

The larva of a large horse-fly, *Tabanus*, (fig. 11) occurs at temperatures up to about 100° Fahr. in the thermal waters of Yellowstone Park, where I have found them in several places. This same species (*T. punctifer*) breeds in alkaline water and related species develop in salt-marshes, as for example the common "green head" of the Atlantic seashore.

Fig. 12. Brine-Fly, *Ephydra*

The larvæ of members of this genus develop in brine pools, salt lakes, alkaline ponds and warm springs.

Perhaps the most remarkable Diptera to be mentioned are the larvæ of *Ephydra*, small flies (fig. 12) which develop in saline pools, even in the extremely salty water of the Great Salt Lake. There are numerous species, some of which are unable to develop in fresh water, and one has been found in warm springs in Yellowstone Park.

Several other orders of insects are repre-

FIG 13. CADDIS-WORM CASES

The larvæ of certain caddis-flies occur in thermal water. The photograph shows two forms from a warm sulphurous pool in Yellowstone Park Attached to one is a small snail shell.

FIG. 14. WATER-BUG, *Ambrysus heidemanni*, FROM SILICA CHARGED WATER AT 96° FAHR. YELLOWSTONE PARK

FIG 15 AMPHIPOD CRUSTACEAN, *Gammarus limnaeus*. THE HABITAT OF THIS SPECIES RANGES FROM WARM SPRINGS TO ICE COLD ARCTIC PONDS

sented less abundantly in the thermal fauna, including the preparatory stages of

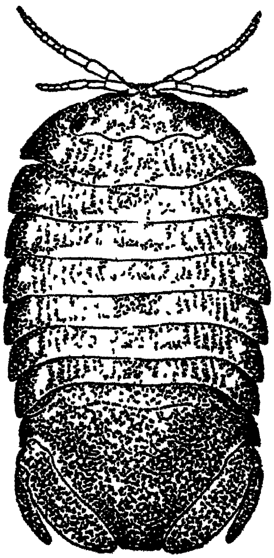

FIG. 16 ISOPOD CRUSTACEAN, *Exosphaeroma thermophilum* FROM A NEW MEXICAN HOT SPRING (AFTER RICHARDSON)

Fossil species of a related genus are known to have inhabited hot springs in Oligocene times.

FIG. 17. SNAILS, A DWARF FORM OF *Physa heterostropha* FROM SILICA CHARGED WATER AT 96° FAHR. YELLOWSTONE PARK

certain caddice-flies (fig. 13), dragon-flies, may-flies and water-bugs (fig. 14).

CRUSTACEA IN HOT SPRINGS

Even a few crustaceans have adopted a thermal habitat. One interesting example is the small amphipod, *Gammarus limnaeus* (fig. 15), which occurs in Yellowstone Park, has been found in a warm stream in Alaska and is widely distributed in cold ponds throughout northern America. It has even been found beneath two metres of ice during June in the far north, indicating a most remarkable tolerance to temperature. A few other crustaceans,

FIG. 18. POND-SNAILS, *Lymnaea palustris*, FROM WARM SULPHUROUS POOL FED BY HOT SPRING. WATER AT 80°–96° FAHR. YELLOWSTONE PARK

such as the copepod, *Cyclops*, and an isopod, *Exosphaeroma* (fig. 16), are known from hot springs. The latter is especially interesting, as a closely related extinct genus is preserved in hot-spring deposits of lower Oligocene age, indicating a long thermal ancestry.

MOLLUSCS IN HOT SPRINGS

Many molluscs, mostly representatives of genera well represented in fresh-waters, are known to inhabit hot springs. Forms of the common *Physa heterostropha* (fig. 17) occur in Virginia, Utah and Yellowstone

Park, and several forms of a related species occur in European hot springs. These snails extend to water of about 106° Fahr. (41°C.). Several species of pond-snails, *Lymnæa* (fig. 18), live in thermal waters in Europe, Iceland and America, invading water of rather high temperature (37°–45°C.). One of these European forms apparently cannot live except in water above 27°C.

the writer in Yellowstone Park (fig. 19). There he found the tadpoles of a frog (*Rana*, probably *R. temporaria pretiosa*) in water ranging between 104°–106° Fahr. This is several degrees above the temperature at which unacclimatized frog and toad tadpoles succumb to the effects of heat, and seems to demonstrate unequivocally that acclimatization of amphibians may take place.

FIG 19 OVERFLOW FROM HOT SPRING NEAR YELLOWSTONE LAKE. SNAILS AND TADPOLES INHABIT THIS WARM STREAM

VERTEBRATES IN HOT SPRINGS

As mentioned on a previous page, certain vertebrates must be counted as members of the thermal fauna. A few fish live in hot springs or streams, usually remaining away from the surface of the latter, where the temperature is higher. They are rarely seen in water over 25°–30°C. and apparently none can survive temperatures of more than about 40°C. (104° Fahr.) even for short periods.

An interesting case of adaptation to thermal water by an amphibian was noted by

GENERAL CONCLUSIONS

Many additional cases relating to diverse animals might be cited, but the foregoing summary is sufficient to illustrate the variety of the thermal fauna. It shows also that this fauna is of secondary rather than of primordial origin. The absence of typically marine kinds indicates that it has arisen mainly through the migration of forms from fresh water. Furthermore, the preponderance of species related to ones that have migrated into a marine or semi-marine (brackish) environ-

ment indicates that thermal and saline situations have imposed similar obstacles to the biota which has entered them from fresh water. These depend undoubtedly upon the presence of salts in solution and the attendant rise in the osmotic pressure of the medium. High temperature is a deterrent that has been overcome by acclimatization, ordinarily, however, within quite narrow limits, especially in the case of animals, which are able to endure much less heat than plants. An added inconvenience is the rather consistent dearth of dissolved oxygen in thermal waters, which renders respiration more difficult for purely aquatic animals.

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THE LOCALIZATION OF DEVELOPMENT FACTORS

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THE PLACE OF EMBRYOLOGY IN GENERAL BIOLOGY

EMBRYOLOGY is the science that studies the embryological development of living beings and endeavors to determine its causes and mechanisms. Owing to these goals it holds an important place in general biology, and the first section of this article will be devoted to the precise statement of this place.

Life is, according to all evidence, a continuous phenomenon; it has proceeded, uninterrupted ever since its appearance on earth in remote geological times. Never, in fact, has the spontaneous generation of living beings been observed, and no man of science now has any doubts regarding the non-existence of this phenomenon. Life always appears to the observer or to the experimentalist in the shape of simple or complex living beings; to the continuity of life is opposed the discontinuity of living beings, of the organisms themselves. For, as a general rule, every organism is called into existence, goes through an adult state, then dies; exemption from death of some lower organisms has not yet been demonstrated, although some recent investigations make it seem at least likely. (Calkins, Woodruff, etc.)

In reality, in most cases—we may even say, in all animals—continuity of life is secured by the phenomenon of reproduction; we mean that every being before dying or while dying gives off germs able to reconstitute a being similar to the one from which it came and to perpetuate in that way the species to which it belongs.

Reproduction in animals—we shall not give our attention to plants where the facts are essentially the same—may doubtless assume various shapes, but sexual reproduction prevails above all, for it involves the entire problem of the actual origin of living beings. Agamous reproduction, viewed in all its bearings, is but one of its corollaries; and parthenogenesis, the development of an egg without the intervention of a male element, is either relatively uncommon or but a precious laboratory technique used to analyze fecundation; in any case it raises the same general question as sexual reproduction.

In every generation, every time a new organism is brought to life, the biologically fundamental question is put: what are the factors by whose action a fecundated egg, a zygote—whose structure is morphologically that of a simple cell—can, by a series of transformations and differentiations accompanied by growth, become a new being, identical in all its characters with all the representatives of the species to which it belongs.

The problem, viewed in a concrete way, may be stated as follows: the fecundated egg is a cell; as such it lives and displays all the physiological properties of living matter: it breathes, it feeds, it divides, it grows, etc. But it has also a peculiar physiological property: the natural and unavoidable consequence of its vital ac-

tivity is to give birth to a new organism. Now this particular property of the egg must have its substratum in its own substances although it cannot be anatomically perceived, and it is necessary to seek in that egg for its localization, its constitution, its real properties.

Every egg when it is fecundated is a complete cell and anatomically it is nothing else. It possesses a nucleus, whose chromosomes have been contributed half by itself and half by the spermatozoon, which is exactly like that of any normal cell of the species. It possesses a large cytoplasmic body laden to a various extent with nutritive matter, mitochondria, a Golgi apparatus and a centrosome which comes probably from the spermatozoon. I cannot here describe the evolution it has followed to reach this state,—its ripening, the ripening of the spermatozoon, fecundation—in spite of the great interest of these processes (see the book by E. B. Wilson). It is enough for us to take as a basis the fecundated egg ready to develop, that needs for this purpose only the usual exterior conditions: temperature, humidity, oxygen, etc.

Now a simple observation of facts, without using special experimental technique, has shown long since (Whitman, Rabl, Van Beneden, Julin, Robert, Conklin, etc.) with a great number of species already studied intensively (molluscs, annelides, echinoderms, chordates, vertebrates) that the egg, when beginning development, divides into two blastomeres, whose destiny is determined by the place they occupy in the whole; each of them depending on its position will give birth, by its subsequent evolution, to a determined part of the embryo's body and consequently, of the future organism. Segmentation is then a dividing up of the egg into a mosaic of blastomeres each one of which has its own potentialities and contributes a fixed part to the constitution of the whole body.

SEGMENTATION OF THE EGG

I should like to state precisely this purely descriptive notion with the aid of a few concrete examples, because these will be useful in our discussion, and because they will put in all its fullness the question of germinal localization in the egg. I shall take these examples from among the chordates because facts are clearer there, and also because with them have been carried out most of the latest researches that we shall analyze and that will settle the actual state of the question of the localization of developmental factors.

In the case of the tunicates (Van Beneden, Julin, Conklin) it has been clearly proved that the first segmentation plane cuts the egg into two equal blastomeres: we can follow the further development of these to see that they become, respectively, the right and the left half of the larva. Then the second plane, which is perpendicular to the first one and which cuts in two each of the blastomeres, divides the two half-embryos into two regions with definite potentialities and so on. Conklin especially has been able to follow with remarkable accuracy the cell-lineage of the tunicates in the case of *Cynthia*. The purely descriptive observations have long since received conclusive experimental confirmation (Chabry, Conklin): if we destroy, by means of a puncture, one of the first two blastomeres, the surviving one develops and gives birth to a right or left half-embryo. We can infer from these facts that the fecundated egg of the tunicates has a bilateral symmetry; it is made of two halves which the first segmentation plane separates and which have

their destiny fixed by their own constitution.

The egg of the frog behaves in the same way but with even more interesting variations. Long ago, Roux, after various observations especially involving destruction by puncture of one of the first two blastomeres in the egg of *Rana fusca*, concluded that these two blastomeres are one right and the other left and that they behave as in the tunicates; in consequence the first segmentation plane corresponds to the plane of bilateral symmetry of the gastrula and the future embryo. This conclusion of Roux and the deep speculative considerations that he drew from it initiated a great number of investigations, some confirming Roux's observations and others contradicting them (Hertwig and others). This controversy is now over; it has been very useful because it put the question of the germinal localization of the egg in its proper place, and gave it the form that it actually has at the present time.

A long series of researches by Roux, Morgan, Schultze, Brachet, etc., has settled, in the particular case of *R. fusca*, a series of very interesting facts, which allow important comparisons to be made with other nearly or distantly related species. I shall give a résumé of them with a few details, but without describing completely the methods used to discover them—that would lengthen this article beyond all measure.

SEGMENTATION OF THE FROG'S EGG

If we examine living frogs' eggs (*R. fusca*) fecundated two or two and one-half hours previously we see that the brown pigment that covers with a compact layer the whole upper hemisphere does not stop under the equator along a regular latitudinal line. In one half of the egg it goes far down, often covering half the distance between the equator and the lower pole; in the other half, the compact pigment scarcely reaches the equator, and between it and the whitish polar regions is a line of gradual transition, assuming the shape of a crescent whose grayish color has won for it the name of gray crescent (fig. 1). The median part of the crescent (its largest) reaches the equator at its upper edge, its horns spread right and left, and below it disappears in-

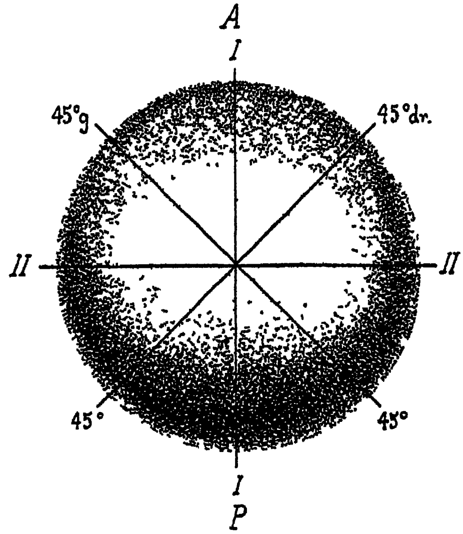

FIG. 1. EGG OF *Rana fusca* SEEN FROM THE LOWER HEMISPHERE SHOWING THE GRAY CRESCENT IN THE UPPER HALF

I-I, plane of bilateral symmetry. II-II, plane perpendicular to the plane of symmetry. 45°dr., 45°g., oblique planes where the first cleavage furrows occur.

sensibly. The gray crescent does not exist in the virgin egg; it becomes visible only after fecundation or after stimulation by one of the agents of experimental parthenogenesis that Bataillon has made known (Brachet). Evidently (fig. 1) the presence of the gray crescent allows us to trace on the egg a vertical plane (from the upper to the lower pole) which divides the gray crescent into two halves and which is consequently a plane of bilateral symmetry; that is to say, it makes out-

wardly visible the bilaterally symmetrical constitution of the fecundated egg. These characters added to its clearness, which is very good in some cases, make it a precious guiding mark for descriptive and experimental analysis.

Now we may consider as perfectly proved that this plane of symmetry of the fecundated egg always becomes the plane of symmetry of the gastrula and the embryo; and the egg is consequently made of a right and a left half which contain in themselves the determinative factors for the formation of the right and left halves of the body.

When segmentation begins, the first cleavage furrow often coincides with the plane of symmetry of the egg and a right and a left blastomere are formed; if we kill one of them, thus reproducing Roux's fundamental experiment, we get a right or a left half-embryo out of the still living blastomere. But it is not always so (Morgan and Boring, Brachet, etc.). Very often the first segmentation plane is oblique to the plane of symmetry. Then the two blastomeres will not have an equal share of the gray crescent substance; one of them will hold, according to the direction and the extent of the obliquity, a whole half and also a more or less big part of the other half (fig. 1). The two blastomeres are then not identical in this respect, although their bulk is the same; and experience shows also that their potentialities are different; the destruction of the one does not cause the other one to develop into a half-embryo.

To sum up the results of the experiments, we may say that the quantity of dorsal organs (central nervous system, dorsal chord, mesoblastic somites) derived from a blastomere in a case of oblique division depends on the quantity of material from the gray crescent contained in it according to the position of the first segmentation plane. These ideas will be more precisely stated later; but they allow us already to draw an important conclusion: in the egg of *R. fusca*, the potentiality of the first two blastomeres is not fixed; it may vary within very wide limits. But it may be foreseen, since we can mark exactly the direction of the plane that divides them in relation to the plane of bilateral symmetry which is fixed and immovable.

But whatever is the direction of the first segmentation plane, be it regular, oblique, or perpendicular, the second plane that follows it and that divides the egg into four blastomeres, is always at right angles with it. If then, the potentiality of the first two blastomeres is changeable for reasons already seen, the potentiality of the first four will also be changeable for the same reasons and so on for the further stages of segmentation. Segmentation is consequently but a cutting up of a fecundated egg into cellular regions; it leaves its composition and germinal localizations untouched and this condition continues until the localized substances begin to display their own potentialities. Since the gray crescent is only a part of the cytoplasm of the egg, and since it determines the destiny of the various regions of the egg, it follows that the first determination does not occur in the nucleus, but instead appears in the cytoplasmic composition of the egg-cell.

LOCALIZATION WITHIN THE EGG

These points being settled, we can go further and try to localize in the egg, the regions that will give the different organs of the embryo's body. For this also descriptive and experimental observations of the frog's egg have given very clear results, which is partly due to the fact that the gray crescent remains more or less visible until an advanced stage in segmentation. It can still be easily recog-

nized in the blastula in some favorable cases.

We have been able to recognize, by various methods, the following facts derived from the observations of a great number of authors (Roux, O. Hertwig, Morgan, Kopsch, Brachet, etc.) and they follow the lateral horns of the gray crescent and finally join each other in a caudal lip on the opposite half of the egg, But while this large blastopore is developed, the parts first formed concentrate towards the median plane, growing closer to the caudal lip by a concentric motion.

FIG. 2. YOUNG GASTRULA OF *Rana fusca* SEEN FROM THE LOWER HEMISPHERE

Comparison with figure 1 shows that the blastopore shaped like a horse shoe is formed in the region of the gray crescent.

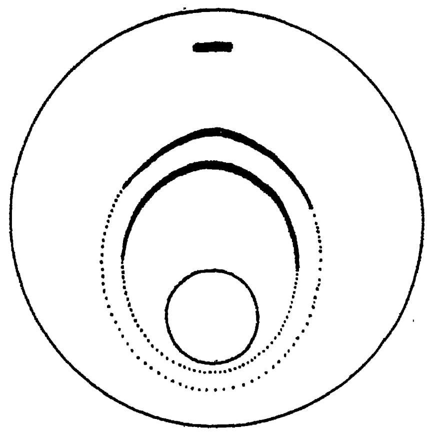

FIG. 3. SCHEME OF THE CLOSURE OF THE BLASTOPORE IN THE FROG

(After Morgan)

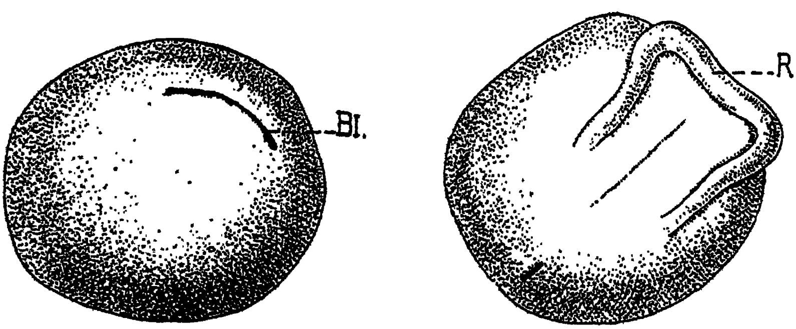

FIG. 4. POSITIONS OF THE BLASTOPORE WHEN IT FIRST APPEARS (AT THE LEFT) AND WHEN ALMOST CLOSED (AT THE RIGHT)

In the space between these two positions the medullary plate is formed. *R*, transverse cerebral fold. (After O. Hertwig.)

recently confirmed by Bataillon, by means of a very clever process: when in *Rana*, gastrulation begins, the position of the blastoporal lip, which appears first—the cranial lip—is found in the larger part of the gray crescent, that is to say, at a small distance under the equator (fig. 2); and as soon as its lateral lips are formed Figure 3, supplied by T. H. Morgan, shows the reasons for this evolution. All the materials of the blastoporal lips taken together constitute a plate which occupies the same area as the blastopore and that may be called the dorsal plate. Indeed it is in that region that the medullary plate, rough cast of the central nervous

system, the dorsal chord, and on both sides the mesoblastic somites from which the myotomes will come, will be differentiated. The anterior portion of the medullary plate, called by embryologists the transverse cerebral fold (fig. 4), which will give rise to the prechordal region of the brain (optical and olfactory regions), will be formed just above the spot where the cranial lip of the blastopore appeared first. The caudal lip of the blastopore will become the anal region.

All this development is naturally accomplished by means of complicated processes concerning whose nature there is as yet no accord; there are emigrations and displacements of material which have just been made known by the works of W. Vogt. But it is not necessary for us to enter into these details: the essential point is, for us, that in *Rana fusca*, the gray crescent, and perhaps the adjacent parts, are the starting point of the processes thanks to which the embryo's dorsal organs, characteristic of every chordate, are formed. The further growth of those organs, their displacements, etc., are secondary facts that will not be discussed in this article. Let us add, to complete the subject, that if the localization of the dorsal organs is determined that of the ventral organs is also determined.

The exact topographic details made known in this article are only valid for *R. fusca;* they may be somewhat different in the other Anura and we shall see that numerous researches, especially by Eycleshymer, Spemann and his pupils, show undoubtedly that they are different in some important points for the urodele amphibians.

In other groups exact localizations have been demonstrated, as we have already said. Especially in the tunicates (that are also chordates) the work of Conklin, to which Duesberg added some interesting facts, made it possible, because of certain details of structure and appearance, to localize the formation regions of axial organs more accurately even than in the frog.

In other animals the existence of the region of a fecundated or segmentated egg, where the developmental factors of the larval organs are localized has been settled for a long time, and everybody knows the fundamental observations on this point of E. B. Wilson on the importance of the polar lobe of the *Dentalium* egg. It is the same also with the ctenophores and even with others where we should least expect it, as with the echinoderms. In reality, we can say that the existence of germinal localizations in the egg or in the blastula is a quite general phenomenon.

The constant existence of localization of developmental factors is certainly a valuable idea, but as we have considered it hitherto it has only a descriptive value, although it has been made obvious by experimental methods; it is a kind of map of evolutionary potentialities, and is only a starting point for a deeper analysis of the real factors of embryological development. The most recent works are devoted to this analysis, as are also the following pages. The first questions are those of the origin, and of the moment and order of appearance of germinal localizations. We are still here in a very dark region and have only scattered information that cannot yet be generalized.

THE RÔLE OF EGG AND SPERMATOZOON

In the actual state of science, we can only determine the real power of a germ when it is allowed to develop, that is, to realize its potentialities. From our standpoint the fundamental property of the egg—one of the greatest riddles of biology—to give birth to a new organism by har-

moniously linked and strictly localized processes, must be submitted to analysis by means of the following questions: (1) what is the rôle of the egg and the spermatozoon respectively in determining localizations; (2) are localized materials formed quickly, abruptly or do they arise slowly and progressively, and: (3) are they immutable or do they change under certain circumstances?

In trying to answer these questions we shall leave the descriptive account of germinal localizations and proceed to the analysis of their nature and real meaning.

Concerning the first question we have already a certain number of interesting and demonstrated facts. It is evident that the egg has in itself everything necessary for complete normal development; for not only are there eggs that have a normal parthenogenetic development, but a great number of others that usually develop after being fertilized by a spermatozoon, may develop by parthenogenesis, if stimulated by some physical agent.

The question is more complex with respect to the spermatozoon; we have a tendency to admit on principle that sexes are equivalent. If this were really true, the spermatozoon, which is but a nucleus surrounded by very little cytoplasm, would also contain the basis of all developmental factors, and the enormous bulk of the egg cytoplasm with all its inclusions would only be auxiliary, particularly nutritive matter, the destiny of which would be entirely directed by the nucleus and the small protoplasmic region that surrounds it. All this is quite likely, but experience must determine whether it is true.

A great number of experiments have been tried with this in mind. Some authors (Yves Delage) thought they had stimulated a "male parthenogenesis" but their results did not withstand analysis. In any case, the spermatozoon acted as an agent of cellular division and could change in only a few points the fate of the cytoplasm into which it had been introduced. I cannot enter into detail concerning those experiments which I have already criticized (Brachet, 1917), but I do not know a surer proof of the limitation of the spermatozoon's potentiality than the results of polyspermy experimentally realized in the egg of *Rana fusca* (Brachet). When this polyspermy is not very pronounced, it brings about a remarkable result. In the voluminous frog's egg, when 5 or 6

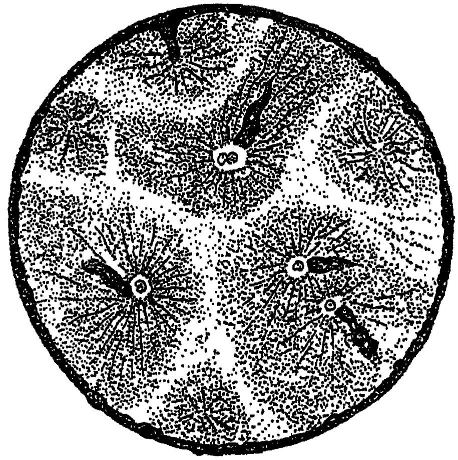

FIG. 5. SECTION OF A POLYSPERMIC EGG OF *Rana fusca* SHOWING MANY SPERMATIC ENERGIDS; IN ONE OF THEM THE PRONUCLEI ARE UNITING

spermatozoa enter simultaneously, but in spots that are rather distant from one another on the upper hemisphere, each one forms in the nearby cytoplasm a spermatic aster and produces what may be called a spermatic energid. Each of these is well separated from its neighbors by clear bands (fig. 5). Each one has a nucleus and a centrosome; one of them, the one that lies at the upper pole, appropriates the egg nucleus (female pronucleus) which unites with that of the spermatozoon. When segmentation begins, in each energid a segmentation

mitosis takes place, exclusively spermatic in all except the one containing the female pronucleus. The egg divides simultaneously into as many blastomeres as there were spermatozoa that entered the egg (fig. 6). Each of these blastomeres has, it is true, two nuclei and two centrosomes, but as segmentation proceeds, a process of regulation takes place and finally all the cells have only one nucleus. This kind of egg develops quite well, produces a normal larva which hatches and may live for some time; such larvae always die,—

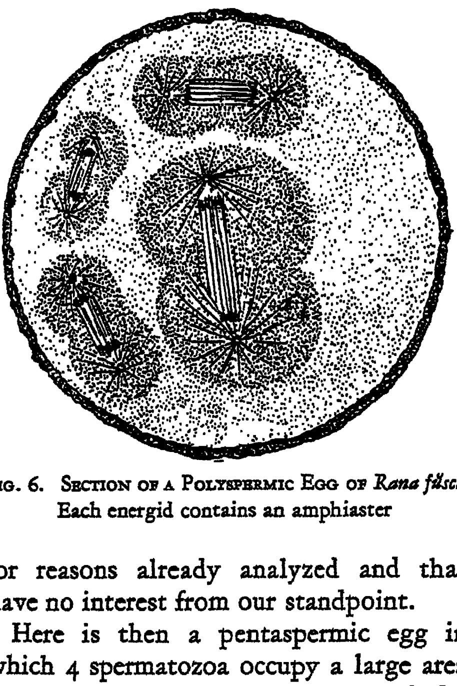

FIG. 6. SECTION OF A POLYSPERMIC EGG OF *Rana fusca*
Each energid contains an amphiaster

for reasons already analyzed and that have no interest from our standpoint.

Here is then a pentaspermic egg in which 4 spermatozoa occupy a large area where they stimulate division and development without any association with the female nucleus. If the spermatozoa had the necessary potentiality to produce an embryo they would, in such an egg, be in an ideal situation to do so, and if those potentialities were even partially realized the egg would become a manifold monster. This does not occur; in the best of cases the egg develops quite normally, the gastrulation is typical and all the embryonic organs form in the normal way. The inevitable conclusion is then, that the destiny of the various egg regions is fixed by their own composition and cannot be changed by the action of a spermatozoon, or, on the other hand, the destiny of a spermatozoon is absolutely dependent on the composition and properties of the ovular cytoplasm in which it has become entangled and the development of which it only helps to initiate. This does not mean that in a normal fecundation the spermatozoon plays no part in the establishment of germinal localizations—we shall later see a proof of that—but it is unable to create them.

This point being settled, the problem becomes clearer and it is in the egg that we must look, first of all, for the primary origin of developmental factors. Let us first see exactly what we know on this point; we shall then indicate the lacunae in our knowledge and what we can expect from further research work.

THE ORIGIN OF DEVELOPMENTAL FACTORS IN THE EGG

In the first place, there are purely descriptive observations, although these are very instructive, made on eggs in which the localization of materials forming the embryo's important primary organs is outwardly visible even before the beginning of segmentation and appears progressively during ripening and fecundation.

A very obvious case is that of the ascidians, especially of *Cynthia partita*, made known by Conklin. During the ejection of polar globules that ends maturation, and the penetration of the spermatozoon, an altering of the cytoplasm takes place; two crescent-shaped, differently colored bands that appear on the surface, superposed and localized in one half of the egg, show externally a

bilateral symmetry which will be the symmetry of the future larva; these enable us to localize exactly the ovular material out of which will progressively be formed the nervous system, the dorsal chord and the mesoblast. We can say that those two bands represent these organs potentially.

Another rather similar case, long studied by Roux, O. Schultze, Morgan, etc., is that of *Rana fusca* whose egg is one of those preferred by experimental embryologists. At the moment of deposition the egg is in the anaphases of the formation of the first polar body. It is then fecundated and, 2 or 2½ hours afterwards, the gray crescent of which we have already spoken and which represents also potentially the embryo's dorsal organs, (nervous system, dorsal chord, mesoblastic somites) appears little by little in one half of the egg. This gives to the egg a bilateral symmetry, the vertical plane of which may easily be identified on the living egg; this is also the plane of bilateral symmetry of the gastrula and the embryo (figs. 1, 2, 4).

In the two instances noted here because they are very characteristic, the outward appearance of germinal localizations and consequently of bilateral symmetry, and the definitive localization of cytoplasmic material coincides with maturation and fecundation.

But there are some cases in which, by observation alone, we can see that the localization of the principal materials is much slower. This is particularly true of a ctenophore, *Beroë ovata*, concerning which Spek (1926) has published a very interesting account. The fecundated egg is covered on all its surface with a coating of hyalin cytoplasm which through the ultramicroscope has a beautiful green hue. From the beginning of segmentation until the 8-cell stage, at every division the green substance enters the cleavage furrow, then when the furrow is completed, it spreads again uniformly over the new blastomeres; its fluidity allows these consecutive movements. But after the 8-cell stage its viscosity increases; when the 8 blastomeres are fully formed the green substance instead of spreading over their entire surface, remains heaped in a determined spot in each of them and so takes a definite position. At the next division, the green substance is nearly all retained by the 8 micromeres, the macromeres keeping only a very small part of it. It is at the expense of the green micromeres that the larva's epidermis and the 8 ciliated ribs of the ctenophore develop.

The localization of the materials of those structures, that helped (cf. especially Fischel) to prove the strictly determinative character of the development of the ctenophore is then slow, and proceeds long after maturation and fecundation. Of course, it is important to note that the substances embodied in the micromeres and determining their destiny, exist with all their properties as soon as the egg is fecundated and probably even before fecundati on; but their final distribution is only completed during segmentation. The substance of the colored crescents in the tunicates and that of the gray crescent in the frog certainly exist also in the egg before maturation and fecundation, but they are scattered in another way, probably more uniformly; they are also localized more quickly and before segmentation begins. We can imagine cases in which localization settling is even slower than in the ctenophores or quicker than in *Rana* and *Cynthia*. This is true, for instance, with *Dentalium* (E. B. Wilson) where the virgin egg has around its lower pole a light region called by Wilson the polar lobe, which is very important from an organogenetic point of view.

EXPERIMENTS ON THE ESTABLISHMENT OF GERMINAL LOCALIZATIONS

This leads us to say a few words about experimental researches on the establishment of germinal localization. E. B. Wilson has stated that if we cut the unfertilized egg of *Dentalium* into two parts by an oblique plane, one of which includes only the polar lobe, the two parts may be fecundated, but the one including the polar lobe is the only one able to produce a trochophore; the other one undergoes only a partial development. There is then already in the egg, at this very early stage, a localization of formative energies. This localization becomes certainly more precise and complete toward the end of maturation and fecundation, but it has been nevertheless largely prepared at earlier stages.

The action of maturation and fecundation is clearer in *Cerebratulus*. In this kind of egg the cutting off of a part of the cytoplasm, before the ejection of the second polar body, does not prevent normal segmentation (Zeleny); if the cutting is done a little later, it causes more and more striking anomalies going even so far as a half segmentation, which is a typical partial segmentation. Even in the sea-urchin, Delage had already stated that if we take off any part of the cytoplasm of the ripe egg, not only is fecundation normal, but also segmentation; nothing seems changed with respect to the egg's potentialities. If, on the contrary, we separate the first two blastomeres from one another, each of them goes on dividing and produces a half-blastula which will be later completed by a secondary change (Driesch).

We could mention other similar instances but those that I have already chosen and that have long been known are sufficient to show that in every egg, between the beginning of maturation and the beginning of development, something happens which establishes in a final way, more or less completely, the substances and energies which will direct the harmony of development and which were until then more uniformly distributed in the egg. And we can foresee some cases in which stabilization is delayed and is only completed at a later stage of development.

We have not been able until now, to specify which of these very important phenomena give to the whole development the direction it must follow, which part is due to the maturation process, and which to fecundation, for most often these processes occur together. In *Rana fusca* we have been able to examine the facts very closely and so have come to some conclusions that are very interesting, although we are not yet able to generalize (Roux, Brachet). We have already seen that a fecundated egg of *Rana fusca*, 2 or 2½ hours after it is brought into contact with the sperm, has its germinal localization finally established and fixed, and that these show themselves outwardly by the appearance of the gray crescent on one half of the egg. Now we can state, by a simple anatomical examination corroborated by Roux's localized fecundation experiments, that the sperm's entrance spot, easily identified because of a trail of brown pigment, is situated in the upper hemisphere of the egg in the half opposite to the one occupied by the gray crescent, and also that this spot is always exactly in the meridian of bilateral symmetry of the egg, which cuts in two the gray crescent.

This constancy would lead us to believe in a predetermination of the entrance spot of the sperm and consequently of the plane of bilateral symmetry. Conklin thinks this is true of the tunicates, but several experiments here show that this is

not the case. These experiments are, first, Roux's "localized fecundations." We can by simply applying a fine silk thread on one of the meridians of the egg, and immersing it in water full of sperms, localize very exactly the entrance spot of the spermatozoa and Roux has stated that in more than 80 per cent of cases there is an exact correspondence between the silk thread meridian and the meridian of bilateral symmetry.

Another proof that looks final is that given by experimental polyspermy. I have shown that in the usually monospermic egg of *Rana* we can easily bring about a simultaneous penetration of several spermatozoa. We can accomplish this by using very concentrated sperm and by rendering the egg's reactions slower by the influence of a $2\frac{1}{2}$ per 1000 NaCl solution for a few minutes. These spermatozoa enter by every possible meridian, we can thus see that there is not a preestablished place of entrance. Moreover, Herlant has observed that when two spermatozoa enter the egg simultaneously, the plane of bilateral symmetry, when it becomes visible, passes exactly between the two fecundation meridians. These proofs seem to settle the question.

But the frog's egg shows even more and allows us to proceed further in the fecundation phenomenon. This phenomenon, as has been stated already orients the germinal localizations. This is an important fact in fecundation, for which I have proposed the name "dynamic manifestation of fecundation." But, in the absence of any spermatozoa, the localization may be brought about by the egg itself. Indeed let us subject an unfertilized frog's egg to the first act of parthenogenesis by Bataillon's methods—puncture with a fine needle, induction shock, etc.—two or three hours afterwards, the gray crescent appears, normally shaped. When we operate with the needle, there is no connection between the plane of bilateral symmetry and the point of the puncture.

The final orientation of the germinal localization is then here purely an ovular phenomenon and it seems to come at the end of a long period of preparation. The egg, under certain experimental conditions, reacts by its own power and establishes its own germinal localization and bilateral symmetry. This shows that the symmetry existed already in the virgin egg but was vague and labile; in normal fecundation the spermatozoon is the determining factor.

It is interesting to remark here that some observations by Just allow us to extend to the echinoderms a great number of the conclusions obtained with the frog.

In the *Rana* egg we can add to the action of the spermatozoa some experimental data which show very precisely that the establishment of germinal localization proceeds with the course of the fecundation process. Experiments show, in fact, that if we take a frog's egg, that has already been in contact with sperm for 30 or 45 minutes, and destroy with a thin slightly heated needle a localized part of its substance, the egg begins to segment, eliminates the part destroyed and produces a perfectly normal embryo. The same experiment made $\frac{1}{4}$ hour later gives a different result; the region of the egg near the part destroyed does not develop as well as the rest and with a quantitative deficiency; the embryo is then asymmetrical although all the organs seem well shaped in it. If we can operate $\frac{1}{4}$ or $\frac{1}{2}$ hour later ($1\frac{1}{4}$ or $1\frac{1}{2}$ hour after the addition of sperm) the result of the injury is the same as the destruction of a blastomere during segmentation; a partial embryo is formed lacking that part of the body that

would normally have come from the destroyed part of the egg (Brachet).

The influence of fecundation on the final establishment of germinal localization is shown by these experiments with sufficient evidence, so that it is useless to discuss the subject further.

MATURATION, FECUNDATION AND SEGMENTATION

But we must now settle the exact meaning of all the facts here related regarding the effects of maturation, fecundation and even segmentation (ctenophores) on the establishment of germinal localization. In reality they do not show us the beginning in the germ of the developmental factors and energies which will be used to build the organs and regions of the body, but simply their localization in some definite spot in the egg. It seems, if we examine our data carefully, as though dynamic and material developmental factors scattered more or less homogeneously in the unripe virgin egg, separate and dissociate the one from the other when ripening begins and even more when fecundation takes place, and settle in spots on the right and left side of a median plane, the normal destiny of which is fixed by their nature and composition.

This localization, whose physico-chemical determination has not yet been successfully studied, may be, according to the species, early, more or less late, speedy or slow, and also, as we shall see later, rigid or more or less labile. In the discussion I have presented here, I have been obliged, in order to give a clear account, to choose cases where this stability, when it is final, is great enough to give segmentation a strict determinative character so that we could assert, on positive facts, that the ontogenetic potentialities of the first blastomeres are strictly determined by the nature and quality of the materials and energies in the fecundated egg, given to them by the direction of the cleavage planes. We shall later speak of numerous cases where regeneration phenomena take place, and where a region of the egg may, under certain conditions, acquire greater morphogenetic potentialities than we would think possible by the quality of its germinal localizations.

In other words, each area of the germ, with its own germinal localizations, has a typical normal destiny, due to what we may call its real potentialities (this expression is equivalent to Driesch's "prospektive Bedeutung"). If with the help of experimental intervention it produces more than its normal destiny, it is because its real potentialities are only a part of a total potentiality ("prospektive Potenz" of Driesch) which will never appear in typical development.

We shall come back later to this point; it was necessary to mention it at this point, because these two kinds of potentiality are connected, by means of a tie not yet discovered by science, but existing nevertheless, with the same differences as stated in the frog, for instance, between the virgin and the fecundated egg; in the one a small loss of substance does not prevent a complete development; in the second, the same loss gives a partial development. We can express this fact by saying that the virgin egg having lost a part of its substance has a total potentiality which the fecundated egg no longer has.

The virgin egg's potentiality (the egg being identical in all its parts) is only due to the fact that the formative materials, the substratum of the developmental energies, are scattered in a more uniform way than in the fecundated egg; they are still more or less mixed and not yet localized in the spots where they will develop. The cutting off of a part of the

egg takes from it a small part of all the materials of future germinal localization and so the deficit is essentially quantitative; the formed embryo will be a little smaller but complete.

This is, at least, the most satisfactory explanation that we can give of these facts; it is simple and may be easily verified by well-conducted experiments. Everything shows, in fact, that the materials and energies of germinal localizations, mixed in the virgin egg, and later localized, have their seat in the egg's cytoplasm and not in the nucleus. When we take off the polar lobe of *Dentalium* or a part of the gray crescent of a frog's egg, the nucleus is untouched and the cytoplasm alone suffers a loss; and the consequences are well known.

THE ORIGIN OF FORMATIVE MATERIALS IN OOGENESIS

But analysis ought to be pushed further, for as I have already said, the question of the primary origin of the egg's formative materials, has not yet been touched in this essay; we have spoken of their removals, of their changes, of their localization which are, in fact, the first stages of ontogenesis. But we have only examined them when their existence was already exhibited by their own developmental properties.

When and under what influences do they arise? When we shall be able to answer this question with objective data, a great part of the enigma of the actual origin of living beings will be explained; but at present we cannot do so. We can only build up some hypothesis resting on presumptions, but nothing more.

The egg of any animal species, when ready to begin maturation,—which is shown by the breaking of its germinal vesicle previous to the forming of the amphiaster of the first polar body,—is the result of a long evolution in the ovary. It was first, as an oogonium, a small cell; it becomes an always large and sometimes enormous cell. During the growth period it is the seat of an active metabolism in which the cytoplasm as well as the nucleus plays a part. The nucleus undergoes at first very complex alterations in its chromatin; the chromosomes unite and prepare for reduction which will be fulfilled during maturation; then it swells, takes the appearance known by the name of germinatal vesicle which it will keep as long as the swelling lasts. Cytologists have minutely described these various phases which have tended to give to the chromosomes the importance they now have. But while these phases go on, the egg grows, its cytoplasm increases; inclusions and reserve materials accumulate; mitochondria increase in number, they shift their places, and take a share in the work of the egg cell. The growing phase of the oocyte is an elaboration period, during which the cytoplasm acquires its material composition, its physical and chemical state and consequently the energy sources which it will use to start development. But we do not know anything of what would interest us here, that is, of the preparations for germinal localizations, except that they are probably carried on at this time. Does the primeval impulsion to this preparation come from the nucleus, as all those authors maintain that localize in the nucleus all hereditary tendencies—which is synonymous of developmental factors—and as Gregoire has recently attempted to demonstrate by purely theoretical consideration? That may be; the nucleus is an active element in cellular metabolism, but the cytoplasm with all its constituents is none the less so, and we cannot say whether one of them prevails over the other.

Our ignorance regarding the physiology

of an important phase of the egg's development comes from an essential cause: the existence of germinal localizations in the egg can only be determined if we make the egg develop. We only know of their existence because we see them differentiate into organs and structures. But up to the present time we have never been able to make an egg develop when it had not yet completed its growth, that is, to a shape where all morphogenetic material is formed and only requires localizing. This localization, sometimes begun during maturation, always made more rapid by fecundation or parthenogenetic processes, in certain cases fulfilled by segmentation, which is in reality the beginning of organogenetic development, is it only possible when all materials have been prepared in the egg?

If we only inferred from what we know at present, we ought to answer in the affirmative; but the confidence that would follow might be premature. In reality, we have never tried to stimulate the development of an unripe oocyte; technical difficulties would be very great; the segmentations discovered by chance in mammalian ovaries (cf. Branca's recent work) are evidently abortive and are not very interesting from our point of view.

But nothing prevents us from hoping for the discovery of new techniques and the goal is important enough to make us look for them. It is, in fact, theoretically possible that the materials of the various germinal localizations are not elaborated simultaneously, but that there may be a kind of hierarchy, be it only of a chronological kind.

If this were so the egg's ontogenetic properties would not only grow uniformly but also increase in number during its growth. In the various stages, previous to the acquisition of its final shape and bulk, it might be different not only quantitatively but also qualitatively, because of the developmental factors it holds. If it were so, and if we could, at those stages, stimulate the development of the growing egg, and make its formative materials give all that they can give, we could get to a dissociation of normal development that would be very interesting and could win back a new interest for phylogenetic considerations resting on ontogenetic characters.

Perhaps none of these experiments may be realized, and any premature development may be impossible, for technical or practical reasons. The origin of germinal localizations can nevertheless be studied by other means: by the general and particular study of chemical composition and physical state of the egg's cytoplasm at various stages of its development. The germinal localizations finally established are only local variations in the composition of the egg's cytoplasm; these variations are as much of a quantitative as of a qualitative kind and consequently as much, and even more, of a physical as of a chemical nature.

We may believe and even hope that the remarkable investigations made these last few years on the physics and chemistry of the cell: cellular constants, viscosity, surface tensions, permeability, etc.—and their variations during vital activity (André Mayer, Schaeffer, Conklin, the Lillies, Heilbrunn, Chambers, Herlant, Dalcq, Vlés, Fauré-Frémiet, Spek, Runnstrom, etc.) may be used as an introduction to a study no longer of the whole but of every separate region of the egg at different stages of its evolution, and so chemistry and physics will help to explain some morphogenetic phenomena. It is a very interesting domain to explore but it belongs almost entirely to the future.

ONTOGENETIC PROPERTIES OF GERMINAL LOCALIZATIONS

In the meantime let us take up again established germinal localizations and let us try to go into the details of their ontogenetic properties; now that we have acknowledged their existence and their importance, it is interesting to know, as far as possible, under what laws their potentialities display themselves. Some important investigations have been published these last few years on this question, making known some very remarkable facts. They were particularly carried out on anuran and urodelan amphibians. Up to this point we have spoken only of the former, because the facts we wished to emphasize are, there, more evident and can be more easily demonstrated; it is now necessary to speak about the urodels which have some important peculiarities and even give to the experiment some possibilities that cannot be realized on the Anura.

Triton has for many years been a subject for the study of causal embryology. Herlitzka's observation has long been classical: he divided the first two blastomeres by means of a hair or silk thread and obtained two well developed twin embryos. In recent years considerable progress has been made owing to Spemann and his pupils (O. Mangold, Hilde Mangold, G. Ruud, Marx, Geinitz).

The essential facts from our point of view are as follows. There is not in the fecundated egg of *Triton* either a gray crescent or any sign that reveals to us, on superficial examination, a germinal localization or a plane of bilateral symmetry; the poles only are easily recognized. Experiments show, nevertheless, as Spemann and Ruud have proved, that these really exist. Indeed, if we separate the first two blastomeres one from the other by Herlitzka's method or any other method of Spemann's school, we obtain two very different kinds of results. Sometimes, each of the two blastomeres develops and gives a normal embryo, smaller of course, by half, and the two embryos only differ in certain details. At other times, one only of the two blastomeres gives a complete embryo; the other one forms a more or less vesicular mass containing neither nervous system nor chord nor myotomes, and consisting only of ventral elements of the body. We can infer that in the first case the first segmentation plane coincided with a plane of bilateral symmetry already existing in the fecundated egg but invisible; that the first two blastomeres are then a right and a left one as in the frog; but instead of giving each a lateral half embryo, an alteration takes place in their substance and each half embryo is completed by producing the half it lacked. This may be obtained also in the frog (Schultze, Morgan) by turning the eggs that are segmentated in two upside down, the white pole being above and the black pole below; the alteration in each blastomere, made necessary by the inversion of the direction of gravity, divides again the formative materials as they are in an egg and two twin larvae develop. These facts may be explained without much difficulty, for the right half of the body is not much different from the left and contains in itself everything that is necessary to produce all the organs in their normal place. It is sufficient to realize the right conditions for a new bilateral, symmetrical balance (Spemann, Brachet). In the second case, on the contrary, the first segmentation plane does not coincide with the plane of bilateral symmetry, but is at right angles with it. It cuts the egg into a dorsal blastomere which contains all the formative materials of the dorsal organs, and a ventral one

which contains only the materials for the future ventral part of the embryo. Here any alteration in the ventral blastomere cannot make it produce more than its germinal localizations allow. There are then in the egg, separated by a plane perpendicular to its plane of bilateral symmetry, a dorsal half containing the localized materials and factors necessary to produce a complete embryo and particularly the dorsal organs, and a ventral half that cannot produce any dorsal organs. Let us remark that it is about the same with the egg of *Rana fusca*, where the dorsal portion of the embryo, when it is taking shape, overruns the ventral half only at its caudal extremity (fig. 4).

Probably in *Triton*, as in the frog, between the two extreme positions of the first division plane with respect to the plane of symmetry: coincidence or perpendicularity, there may be a series of intermediate positions. But as in *Triton* we can only infer them from the results of separating the blastomeres and as these results are intermediate and often difficult to analyze, they are doubtlessly considered as experimental failures.

Summing up, we can say that the egg of *Triton*, either fecundated or segmentated into two, must have a localization of its developmental factors much like that of the frog's egg; but it cannot be directly examined, and that is certainly a disadvantage.

But this disadvantage has a compensation in one property of the egg which opens to the experimental analysis of germinal localization a field that cannot be studied well with the frog's egg; this property is a greater malleability of organogenetic substances, a less irreducible fixedness in the organogenetic properties of the various egg areas. An instance of this has been given already: when in *Triton* the segmentation plane coincides with the plane of first bilateral symmetry, if we separate the right blastomere from the left, each of them gives not a half embryo, but a smaller complete embryo, which is normal except for a certain asymmetry in the inner organs (Spemann) of which I cannot speak here.

The constitutive substances of the right and left blastomere may then easily change their place on either side of a new plane, parallel to the egg's plane of symmetry; they may slide, in a way, towards the right for one and towards the left for the other and reestablish in each blastomere a structure similar to that of the whole egg before segmentation. This alteration is accomplished, normally and easily, because, it seems, each blastomere is isolated and instead of touching its associate along a plane surface, can become spherical. The *Triton* egg shows itself then as a "regulation" egg, to use a well known expression. It is not the only known case; there are many others; for instance, that of *Amphioxus* (Wilson), and of the echinoderms; and for all the same explanation may be given. But there is more still: this power of alteration is present not only in the first two blastomeres; it persists until gastrulation, and the two halves of a blastula can each still produce an embryo.

An important fact to remember is this: that the autonomous alteration can only be brought about with the germinal localizations contained in the blastomeres; it can only establish the materials it contains according to the direction of the first segmentation plane and to the plane of symmetry and probably cannot create any new ones. As a proof of this we see that in *Triton*, if the first segmentation plane is perpendicular to the plane of bilateral symmetry of the egg, the first two blastomeres are not equivalent but always remain different; as has been al-

ready said, the ventral blastomere cannot create any axial organs, while the dorsal one produces a larva containing a complete nervous system, a dorsal chord, mesoblastic somites, etc.

This condition is very important and very likely it can be assumed for all eggs capable of regulation. The possibility of a part becoming equal to the whole emerges from the mystery that certain speculations had wrought around it. It allows us also to link the mosaic eggs, that is, eggs with a strictly determinative development, with eggs capable of regulation, that is, eggs that may undergo some alterations.

In the frog's egg, after destruction of a right or left blastomere, the surviving one always gives a half-embryo unless we turn it upside down; a certain degree of alteration becomes then possible. This shows that the differences between the frog's egg and the egg of *Triton* are not so fundamental as one would think at first sight. The technical impossibility of freeing the frog's egg from its vitelline membrane—an easy operation in *Triton*—does not allow the separation of the first blastomeres; if we kill one of them by a puncture, it remains in contact with the surviving one and may merely by its presence prevent alteration in the other. Nevertheless, McClendon's experiments, although incomplete, in which he could take out one of the two blastomeres while leaving the other in its place, would seem to show that even under much more favorable conditions the alteration does not take place. The question is then still open.

Other facts which we must examine, to complete this discussion, will show us how fruitful and useful for the progress of science is the difference in the behavior of germinal localizations, obtained by experiments, between urodelan and anuran eggs. They will force us to go more intimately into the analysis of the properties of germinal localizations and the real part they play. In the urodels (*Triton*) the very ingenious and well conducted experiments of Spemann, O. and H. Mangold, Ruud, Marx, and Geinitz have shown and explained a series of very interesting facts.

THE "ORGANIZER" AS A MORPHOGENETIC CENTER

Spemann's fundamental experiment, of which the others are merely variations, is as follows: in a triton's egg at the beginning of gastrulation, that is, at the moment when the cranial lip of the blastopore appears, we take off a median fragment of that lip or the immediately underlying part, seeing to it that in the cut off part there be not only elements of the future ectoblast but also of the presumptive endoblast (or ento-mesoblast); if then we transplant that fragment into the ventral part of another egg which is in the same stage or thereabouts, it easily embodies itself in its host and develops. But it not only undergoes its normal self differentiation, that is, producing that part of the embryo's dorsal organs the materials of which it contains; it also acts on the host's cells situated above the implantation spot, which would normally give only ventral organs (epiblast of the body's ventral part, mesoblast of the lateral plates, and digestive hypoblast) and it gradually excites in them, by a kind of induction towards the upper pole, the formation of a rough cast dorsal embryo with nervous system, chord and mesoblastic somites all well formed. The material of the blastoporal region of a young gastrula is, then, able to change the neighboring cellular groups from their normal development and to give them certain morphogenetic properties that

they did not possess, or that at least would have remained hidden and unknown without it. Spemann has given the name of "organizer" to that part of the cranial blastoporal region that can give such a formative impulse, and he considers that "organizer" as a real morphogenetic center which concentrates in itself all the factors that excite development in a triton's egg, the appearance and organogenesis of the dorsal organs characteristic of a vertebrate's larva—central nervous system, dorsal chord, mesoblastic somites, etc.

This conclusion finds also its justification in another experiment which is a kind of counter-proof of the first. It is well known in descriptive embryological research, and W. Vogt has recently confirmed it, that with the urodels and especially in *Triton*, these dorsal organs are topographically formed from the materials situated above the blastopore's cranial lip, between it and the egg's upper pole. We can, then, in the upper hemisphere of the young gastrula, draw the outline of the future medullary plate long before it appears: that is to say, there is a virtual medullary region long before it becomes real.

Now if from that region we cut off a small portion of ectoblast, above the region where the organizer is located, and if we transplant it into the ventral region of another gastrula, that fragment, which in its own place would have become a part of the central nervous system is embodied in its surroundings; it simply becomes ventral ectoblast and later on part of the epidermis lining the inner ventral surface of the body.

On the other hand, a fragment of the ventral ectoblast, which, remaining in its own place, would only become common epidermis, when it is transplanted in the presumptive medullary region of another gastrula is transformed in the new place it occupies into part of the central nervous system.

The conclusion we can infer from these experiments is, then, that in a very young gastrula, the cellular materials which will normally make the medullary plate, the forerunner of the whole central nervous system, do not do so because of a self determination, by self-differentiation; their destiny depends completely on the organizer which is beneath them in the blastoporal lip. This is a real proof that, after all, all developmental factors of dorsal organs are localized in it. These do not undergo a spontaneous but a stimulated development.

It is necessary to remark, though, that Goerttler has recently expressed doubts on the absolute indifference, in early stages, of presumptive medullary materials, in *Triton*. By means of a different method from Spemann's, that of punctures producing localized destruction, he has been able to observe a slight medullary differentiation of those presumptive elements even while depriving them of the organizer's influence. They would then be already in some way predetermined before they come to occupy their final location. This reservation made by Goerttler, if it is verified, has a far from negligible importance. But the importance of the organizer as the center of a differentiation from a distance would still be very great.

Finally, the analysis of the organizer has been continued in recent years by Geinitz, who has demonstrated the fact of its negative, or, at least, relative specificity. We knew already from the investigations of Spemann and H. Mangold that the organizer of a species of *Triton* could act on the germ of another nearly-related species. Geinitz has shown that these results can be extended to other urodels; the organizer of *Pleurodeles* or of

Axolotl implanted in the young gastrula of *Triton* produces in the host a secondary embryological rudiment. But what is most unexpected is that the organizer of an anuran, particularly of *Bombinator pachypus* acts exactly in the same way; it not only undergoes its own self-differentiation, but it produces by induction a development of dorsal organs in the triton material in which it is implanted. This observation is very interesting biologically, but it makes necessary certain remarks the importance of which will be shown later.

What Geinitz calls "organizer" in the Anura is the region situated just above the upper blastoporal region; and indeed this behaves like an organizer when it is implanted into the ventral region of a triton gastrula. But we shall see later on that the anuran organizer is localized long before the blastopore appears, and, at the stages when Geinitz operated, its action on the egg had been long felt, perhaps it was even at the end of its inductive power. This is probably the reason for Geinitz's observation, although, under very difficult experimental conditions, an urodelan organizer implanted into an anuran gastrula does not excite any development and only undergoes its own self differentiation. In fact this stage is in the Anura too much advanced; the evolutive determinism of the different regions is already fixed and can no longer be changed.

It is clear, nevertheless, that there is in this field, matter for new research work that may give very interesting results.

Two more points must be noted to complete the analysis of the investigations of Spemann and his collaborators. One is a quite obvious fact: in the organizer the essential part, from the standpoint of its morphogenetic action, is the entoblastic region; the ectoblast is by itself ineffective. Marx and Geinitz have recently given some new proofs of the part played by the dorsal endoblast (endo-mesoblast) in the differentiation of the medullary plate at the expense of the ectoblast that covers it: these proofs confirm the earlier observations of Spemann and Mangold.

The other point, established and confirmed by various experimental combinations of Spemann's school, is of a chronological kind. All the experiments on *Triton* here described only give complete results when the egg has arrived at the stage at which the researches were made: the young gastrula with a barely outlined blastoporal lip. A little later, when the blastopore is completed and has shrunk into a long slit, the developmental determination of the germ's various parts is fixed. The ventral ectoderm no longer reacts in the presence of an organizer; it continues its normal development; a presumptive medullary plate fragment implanted in the ventral part is no longer altered under its influence and produces what it would have produced if it had been left in its place. The advanced gastrula has become a mosaic of potentialities that can no longer be altered. This fixation could naturally be foreseen; it was nevertheless interesting to determine, by experiments, the exact moment when it occurs.

But there is another question not yet answered. Is the organizer, which occupies the region of the cranial blastoporal lip at the beginning of gastrulation, localized in that exact spot since the beginning of development, and was it already in that same spot with all its potentialities in the fecundated egg? Or is it the result of a concentration, in that same spot, during the stages that immediately precede the gastrular invagination, of materials scattered in a region that is larger in the transverse direction, near the equatorial region of the egg?

Goerttler's observations by means of Vogt's method of vital staining, and others described by Vogt himself, seem to show the second alternative as more likely. These authors have noted, in fact, when gastrulation is beginning, some cellular movements that seem equivalent to a real establishment of primordial rudiments, and it is then quite likely that the stage which Spemann studied is preceded by others where morphogenetic factors are differently scattered over a larger region.

It ensues from this that the final establishment of those factors, characterized by the formation of the organizer of the dorsal organs, is in the urodels a slow process that ends rather late. Already, in the first pages of this paper, have we remarked that, as a result of Spek's latest researches, the same localization in the ctenophore egg is established much earlier, although it is only ended in the 8-blastomere stage. We have insisted on the fact that in the Anura it is earlier still, since it seems to be established and finally fixed with all its characteristics as soon as fecundation is realized, and is made obvious by the outward appearance of the gray crescent. This explains many differences between the results of experimental interventions with the Urodela and the Anura, and it allows us in the latter, to discover new and more general properties of germ localizations, that are seen with great difficulty in the urodelan egg.

In the Anura and especially in *Rana fusca*, of which I shall particularly speak, the normal development of the embryo is a little different from what it is in *Triton* and in a general way in the urodels. In these, where the appearance of a prominent blastoporal lip is the first topographical mark allowing a localization of the rudiments, the greater part of the embryo's dorsal region is formed above it, towards the upper hemisphere. This has been shown by the researches in descriptive embryology, and the experimental work of Spemann has given what seem to be final proofs. In the frog, where an early exact mark is furnished by the gray crescent, numerous descriptive and experimental studies, that we have already briefly described and that are fully confirmed by recent results of which I shall speak later, have shown that the gray crescent contains the rudiment of the region that, at the moment of gastrulation, the upper (cranial) lip and the neighboring parts of the blastopore's lateral lip will occupy.

Later on these lateral lips will spread and reach the lower pole, near which they unite into a lower caudal lip. But while it spreads in this way, the blastopore becomes closed by a concentration of its cranial and lateral lips; as the end of this concrescence the blastopore is reduced to a small hole in the caudal extremity (fig. 4) all along that closing line, and at the expense of the cellular materials of the blastoporal lips (that is, of the gray crescent, and of the regions that are its prolongation towards the lower pole) an ecto-endoblastic plate is formed which produces the dorsal surface of the primary intestine and in which will be formed the rudiments of the central nervous system, the chord, the epithelium of the digestive tube and the mesoblastic somites. We can then say that the body of the *Rana* embryo is of blastoporal origin; only the prechordal fore-head, that is to say, the region of the fore-brain characterized by the optic and olfactive regions, is formed out of the cranial lip, towards the upper pole. It is the only part of the body that is formed, in the frog, according to the urodelan manner: from below to above; all the rest is made in the other direction, from above to below. Notwithstanding

the reservations made recently by Vogt on the absolute exactness of these facts, we can consider them as the more solidly established because they exactly correspond to the results of recently published experiments (Brachet, 1923).

RESULTS OF DESTROYING CELLS OF THE GRAY CRESCENT

In certain frogs' eggs the gray crescent is perfectly visible, and although segmentation hides a part of it, it still remains visible in the blastula, a few hours before the blastoporal lip begins to rise. We can then destroy, with a small slightly heated needle, a part of the blastular region covered by the gray crescent, either in the middle, or in one of its lateral horns. The group of cells destroyed by the needle or the heat, is for the greatest part ejected from the egg after a few hours and a scar is formed. A few dead cells remain in their place, and allow us sometimes, even 48 hours after the operation, to recognize in the embryo the injured spot.

The aim is to prevent or alter the development of the potentialities of the cells in the gray crescent; and we can see at once that these kinds of experiments are in fact the reverse of those Spemann and his collaborators have applied to *Triton* in more advanced stages.

The results of these experiments, varying in proportion with the intensity and localization of the puncture, but remarkably linked together, allow us to draw the following general conclusions. The median part of the gray crescent, which is also the largest (fig. 1) and which is cut in two by the blastula's bilateral plane of symmetry—which is also the egg's plane of symmetry—and where the blastopore's cranial lip will later arise, is the only part liable to undergo an autonomous differentiation, that is to say, that its development seems only due to the forces it has in itself; it only gives the fore part of the head's chordal region. But the activity developed in that important spot is really the initium of all the embryo's dorsal morphogenesis; it stimulates progressively, by a real induction, the differentiation of the materials situated above it, for the formation of the prechordal head, and to a greater extent, the differentiation of the elements of the crescent's lateral portions as well as their prolongation towards the lower pole, which will form the nape of the neck, the trunk and later on the tail.

This nodal point formed by the middle part of the gray crescent gives then the condition of progress for the potentialities held in the gray crescent's lateral horns, and in a more general way, of all the blastula's materials which will help to form the embryo's dorsal organs. It behaves, as Spemann says, as an organizer; it has from the morphogenetic standpoint the same value as the region surrounding the upper lip of the triton blastopore. This organizer of the frog's blastula is nothing else than the middle part of the gray crescent of the fecundated egg; for this reason we cannot doubt that if the blastula's localized destruction could be realized on the fecundated egg, the same results would ensue.

The experiments here related show another important point. Under the conditions in which they have been performed, we can clearly see that the organizer of the frog's egg can only induce already predestined materials to develop, it has no influence on other materials. This is another difference between the frog's egg and that of *Triton* and it explains Goerttler's failures in his transplantations of the triton organizer into frog blastulas. It is possible, though, that if Goerttler had tried implantations

on earlier stages he might have obtained very different results. Such verification experiments are, however, very difficult to perform.

There is another kind of fact which gives us some idea regarding the remarkable properties of the germinal localizations in the frog's egg. If, for instance, we prick with a heated needle the gray crescent substance a little to the right or left of its middle part, and if the injury is sufficient to destroy all the active material —or material activated by induction— no organ is formed either at the level of the injured spot or at the back of it. Nevertheless the blastopore's lips arise on either side; but while on the healthy side the lip material differentiates into a nervous half-system, a half-chord, a row of somites, all well-made and normal, on the injured side no organ is formed and in all the blastoporal lips down to the rudimental of the caudal bud there is only a cellular proliferation. This kind of embryo never lives longer than three days after the operation.

If the destruction of the gray crescent material is only partial, the formative induction can progress. But it is weaker and we can still see on the injured side a central nervous half-system, a half-chord, and a row of somites, but they are much smaller than the normal ones; they are like miniatures of normal organs. They may, nevertheless, be perfectly well made and undergo their normal histogenesis (fig. 7) if they can acquire a sufficient bulk.

Evidently, if we perform a great number of experiments, we can obtain a great number of quantitative variations between the total suppression of morphogenesis and a complete and normal morphogenesis, we can obtain a whole series varying in degree. But the conclusion we draw from them all is that the bulk of the organs differentiated by induction is in proportion to the bulk of the cellular body.

This quantitative idea becomes even more interesting if we state that the deficiency produced in this way in the dimensions of the organs is indelible and can never be won back. We can, in fact, keep alive, for several days after the operation, larvae that have undergone a unilateral (right or left) lesion if not too serious and which have on that side a nervous half-

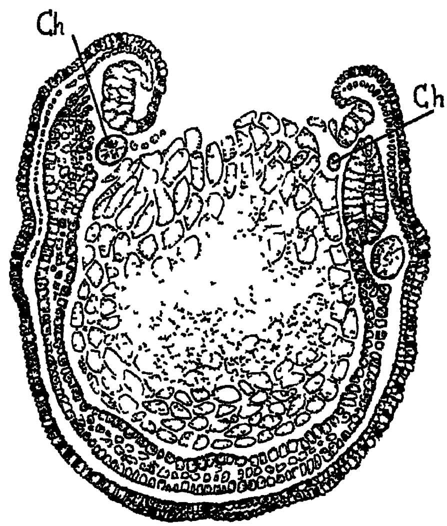

FIG 7. SECTION THROUGH AN EMBRYO OF *Rana fusca* DEVELOPED AFTER THE PARTIAL DESTRUCTION OF THE RIGHT HORN OF THE GRAY CRESCENT IN THE BLASTULA STAGE

On that side the nervous system and dorsal Chord (*Ch.*) are much smaller than on the uninjured side.

system greatly reduced in bulk but not in length, a series of somites and eventually even a dorsal chord. At that moment these larvae are small tadpoles, freely living in water, provided with gills, a normal heart, and freely circulating blood. The two halves of the body are identical; they are normal in length, and have both undergone their functional histogenesis, but the reduced side remains smaller and does not win back anything it lacks, although the conditions of recuperation if it were possible, are well provided.

LIMITS TO GROWTH

This statement brings up the question of the growth of the organism and of its limits and consequently the reasons for the limitation in the length of the organism. The fact that organs formed with too little initial substance remain small and can never win back what they lack, shows that the materials they are made of, have a limited growing power because of their composition, that is, of the quantity of inductive substance they have received. This can only grow by nutritive assimilation within definite limits. It is as though the substance wears away during morphogenesis without being reconstituted by assimilation. As the organogenetic regions already exist in the frog with all their properties in the fecundated egg, we may infer this simple but important formula, that the fecundated egg of *Rana fusca* contains in itself, in its own substance, the conditions limiting the growth of the organism that will develop from it. Germinal localizations are then not only the material and dynamic substratum of embryological organ-differentiation, but rule also the size of the adult animal.

The reader will see from all this that the researches on anuran and urodelan amphibians do not contradict one another as some people think, but on the contrary, they complement one another. Each of the two groups furnishes good material for study, exhibiting very luckily for scientific progress, similar phenomena in different ways: in the anuran egg germinal localizations occur very early and are quickly fixed and established; the possibilities of alterations are, for them, very early inhibited, perhaps simply owing to the too great viscosity of the cytoplasm. In the urodels, these same processes being much slower, are only finished when gastrulation is in an advanced stage; alterations in germinal localizations are possible until then and the determination of the germinal regions is only then fixed; this probably is due to a lesser viscosity in cytoplasm. In all the species studied up to the present time germinal localizations, with some variations, may be compared to the anuran or urodelan type or else may be intermediate between the two.

PROBLEMS OF THE NATURE OF GERMINAL LOCALIZATIONS

In this essay the actual state of germinal localizations has been set forth as it appears to the author according to the most recent investigations. We have refrained, as a rule, from any speculative, theoretical view, and have kept to facts of experiment and observation and the conclusions we could justly arrive at from them; we have been able to link them in a coherent whole which is at least good in this sense, that it gathers together problems not yet solved and clearly organizes data regarding them. Although the work already done is, from this standpoint, encouraging, and even satisfactory, it furnishes only the first steps on a road that remains broadly open to science. We know that developmental factors exist and that they are localized in the germ; we sometimes obtain a view of the establishment of these germinal localizations; we know some of their properties, but we know nothing as yet of their intimate nature. The most important study, still to be undertaken in science, is precisely the investigation of the nature of the germinal localizations and for the elements of the germ from which they are derived. Germinal localizations, which are specialized zones in the egg, have certainly a peculiar chemical composition and physical state; each

formative zone must have its own formula that differs from the others quantitatively and qualitatively, and it should be possible to make a graphic outline of the variations it undergoes during all its evolution. The superposition or combination of these studies, when they are made, will be the physico-chemical expression of embryological development. This analysis will require much time and work, but it must be done to help the progress of science. Without waiting for that result, embryologists who are interested in the biological aspect of their science,—and they are more and more numerous—have still an important program of analytical research.

The germinal localizations here discussed are the fundamental localizations that can be traced back to the egg. They are those that contain the materials and energies destined to produce, not one organ or one system of organs, but a whole region of the body. We may recall in fact, that the most exact data have been acquired by the study of the formative centers of the dorsal organs of amphibians. Factors that are localized and recognized are really factor complexes and we ought to dissociate them into their elements, and then see the reciprocal actions among them and between them and the rest of the germ. From this standpoint Hoadley has recently published some very interesting researches on the blastoderm of birds. The primordium from which the eye will come, for instance, has a different development if it is isolated and transplanted in the allantoic chorion of another chicken's embryo; the development depends on the stage of the germ's development at the moment of isolation. Its potentialities are not all simultaneously established; they come progressively in a certain order; at the beginning this primordium can only produce a vesicle whose cells are colored by a pigment; a little later it can produce a rudiment of a secondary vesicle, that is to say, invaginate with the rudiment of a visual sheet, and so on. Hoadley has made similar observations for other organs also, and particularly for the excretory apparatus.

We do not know how far these observations may be used for generalizations, but the notion that each germinal localization, creating an organ system, still undergoes an inward development after it has appeared, is worth notice. It is likely, though, that observations will show that this movement may be rapid or slow, depending on the species; in some the localization will appear together with all its properties, in others we shall be able to catch by experiment the various stages of their succession; this is true for the final establishment of the great germinal localizations in the egg of the Anura and Urodela.

Besides the interesting problem of developmental factors, which is the only problem discussed in this paper, there are a great number of recent investigations on the development of the branchial apparatus, of the heart and especially the limbs, to which Harrison and others after him have devoted a series of remarkable investigations. But these are outside of our province.

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THE VISCOSITY OF PROTOPLASM

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GRAHAM, the founder of colloid chemistry, called the viscosimeter a colloidoscope. He felt that the problems involved in the study of colloids were most intimately bound up with the changes in their viscosity.

At the present time the physical chemist can study the properties of colloids in a number of ways. But for the investigator of the colloid chemistry of protoplasm the measurement of viscosity is at present almost the only means of approach.

The physical and chemical study of protoplasm is never easy. The intrinsic difficulties are obvious. The colloid chemist has large masses of material at his disposal, but the biophysicist must be content with droplets too small for ordinary vision. Moreover in the manipulation of these microscopic droplets he must be extremely cautious. Almost anything he does is likely to cause death, and once this occurs the protoplasm is no longer protoplasm.

Small wonder then that for so many years students of the living cell were content to do their physical thinking in terms of loose, general speculation. It is much simpler to argue about the physical properties of protoplasm than actually to measure them. But the physical study of protoplasm is by no means impossible. The biologist may never be able to make measurements with the precision which the physicist is able to employ in his study of easily accessible inanimate objects. On the other hand measurements can be made and they are being made.

METHODS OF MEASURING VISCOSITY

Perhaps the pioneer in the viscosity measurement of protoplasm is the German botanist Heilbronn. Before him various biologists had observed the flow of protoplasm and had used rough descriptive terms in discussing its viscosity. Reinke (1895) and Albrecht (1898) noticed that the flow of protoplasm from crushed sea-urchin eggs was slower after fertilization. Workers using the centrifuge in studies of the organization of the egg and the potentialities of its parts, commented now and then on the fact that granules moved through the egg more readily at certain times than at others. Indeed Fauré-Fremiet (1913) emphasized the important point that there were differences in viscosity in the protoplasm of the eggs of *Ascaris* at different temperatures. But it rather seems as though Heilbronn was the first to systematically attempt real measurements of the viscosity of living cells. He observed the speed with which starch grains fell through the protoplasm of certain plant cells. His first studies were on the cells of the leguminous plant *Vicia faba* (1912, 1914). From a comparison of the speed of fall of the starch grains in protoplasm and in water, Heilbronn was able to determine the protoplasmic viscosity. The method that Heilbronn used depends

on well known physical principles and is in fact a standard type of viscosity measurement.

At about the same time that Heilbronn was beginning to measure the protoplasmic viscosity of plant cells, another type of viscosity determination was being undertaken for animal cells. Kite (1913) very cleverly applied the Barber pipette method to the microdissection of cells. Using extremely fine needles, he cut into a wide variety of cell types under various conditions and by watching the progress of the invading needles he attempted to make estimates of the viscosity. Kite's estimates were never in any sense measurements. He described certain cells and parts of cells as gels, others were sols, and some of the cellular gels he thought of as being stiffer than others. The work of Kite was later taken up by Chambers (1915, 1917a and b, 1919) and then by Seifriz (1918, 1920, 1921). The latter tried to introduce a scale of viscosity values by comparing the passage of a needle through protoplasm and through various chemical substances. This was really an attempt to make microdissection a quantitative measure of viscosity. The possibility of the success of such a procedure is rather doubtful. That anyone should be able to measure viscosity accurately by observing the passage of a mechanically controlled needle through a fluid seems on the face of it unlikely. It would be very easy to put the matter to a test. If a microdissectionist were given certain unknown samples of fluids, it would be interesting to see how his estimates of their viscosity compared with the known values.

As a matter of fact the estimates of viscosity furnished by most microdissectionists are probably based largely on their observations of the speed of flow of protoplasm from punctured cells. If this is the case the method is not fundamentally different from the older type of work in which biologists studied the escape of protoplasm from crushed or compressed cells and estimated its viscosity by receiving a mental impression of the speed of flow. Used in this way the microdissection method may serve as an indicator of large changes of viscosity, provided that the reaction which occurs at the surface of the emerging droplet of protoplasm is the same during the progress of the experiment. As protoplasm emerges from a cell it immediately becomes invested with a film. In a paper now in press (1927) I have called the reaction which occurs at the surface of emerging protoplasm the surface precipitation reaction. I have found, moreover, that the reaction varies widely under various external and internal conditions. A thorough understanding of this reaction may contribute to a greater precision of the microdissection method. Until such an understanding is reached we can never be certain of which factor is involved in the speed of escape of protoplasm from a punctured cell. If for example the protoplasm flows out very slowly, this may be due either to a lowered viscosity or it may be due to an increase in the speed of the surface precipitation reaction.

The gravity method of Heilbronn, although very useful for certain types of plant cells, can not be employed for the determination of the protoplasmic viscosity of animal cells. For these cells a force greater than gravity must be used to move the granules through the protoplasm. Centrifugal force serves the purpose very nicely. With the aid of a centrifuge it is often a very simple matter to throw the granules of a cell to one pole. The speed of the granules can then be determined with a moderate degree of accuracy, and in this way it is possible to obtain a meas-

ure of the viscosity. The technique of viscosity measurement by the centrifuge method has recently been described in detail (Heilbrunn, 1926a).

In addition to the gravity and centrifuge methods of measuring protoplasmic viscosity, several other types of measurement have been employed. Heilbronn (1922) devised an ingenious magnetic method. He introduced iron particles into the protoplasm of slime molds and measured the speed with which they were attracted to an electromagnet. This method, as Heilbronn himself points out, is probably not generally applicable, for large metal particles could scarcely be introduced into other types of cells without injury.

Several authors have observed the Brownian movement in protoplasm and have estimated the viscosity from the rapidity of such movement. Ordinarily this has been done by watching the protoplasm under darkfield illumination (Leblond, 1919; Bayliss, 1920). Such observation can furnish evidence as to very pronounced changes in the viscosity of the material in which the protoplasmic granules are suspended.

It is also possible to determine the speed of Brownian movement in another way. When cells are centrifuged the granules thrown to one end of the cell slowly migrate back to their original position. The speed of such a return migration depends in part at least on the speed of the Brownian movement. By measuring the rate at which the granules return one can obtain a measure of the protoplasmic viscosity. Unfortunately, however, the linear distance traversed by a particle in a given time varies inversely not as the viscosity itself but as the square of the viscosity (see Burton, 1921). The method is therefore not a very delicate one, although it does have certain advantages. A few preliminary measurements have been made with it.

Finally mention should be made of the plasmolytic method of estimating protoplasmic viscosity. This has been developed by various botanists (Weber, 1921a, 1924a, 1925a, b, c, and d; Cholodny, 1924; Scarth, 1924a). When a plant cell is placed in a hypertonic solution it usually shrinks from the cell wall in a round or oval mass with a smooth contour. This Weber designates as *convex* plasmolysis, and it is an indication of a relatively low viscosity of the interior protoplasm. Following an increase in the protoplasmic viscosity, the plasmolysed cell may show instead of a smooth contour, an uneven rough border ("eckige Plasmolyse"), or it may retain attachment to the cell wall by strands of protoplasm ("Krampf-Plasmolyse"). Such formation of strands is in part due to an increase in the adhesive properties of the surface layer of the cell. In *Spirogyra*, an increase in the rigidity of the chromatophore may cause a type of plasmolysis which is called "Schrauben-Plasmolyse." That these different types of plasmolysis are really associated with changes in the viscosity of the interior protoplasm has been demonstrated by Weber. By centrifuge tests he has shown that when convex plasmolysis occurs, the viscosity of the protoplasm is relatively low. Following coagulative changes in the interior of the cell the plasmolysis changes from the smooth convex type to the uneven or "eckig" type.

Further discussion of the methods of viscosity measurement for living cells is scarcely necessary. An excellent review of the entire subject has recently been published by Weber (1924b), and the reader is referred to this source for further details.

It should be pointed out, however, that the various types of viscosity determination are not always concerned with the

same thing. Thus if one estimates the viscosity from the speed of Brownian movement of a granule, the viscosity value arrived at is not so much that of the entire protoplasm but rather that of the medium between the granules. On the other hand the gravity method, the magnetic method, and the plasmolytic method should give values which represent the viscosity of the entire protoplasm, granules and all. Probably this is also true for the centrifuge method (see Heilbrunn, 1926b), although this method may give a value intermediate between that of the entire protoplasm and that of the fluid between the granules.

VISCOSITY OR PLASTICITY

Perhaps it is not quite proper to speak of the viscosity of protoplasm. It may be that protoplasm generally is a plastic solid rather than a viscous fluid. If this were the case it would be more correct according to some authors, (see for example Bingham, 1922), to speak of its plasticity rather than its fluidity or viscosity.

Many materials that we ordinarily regard as fluids are really plastic solids. Paint, for example. When subjected to only a slight force, plastic solids do not flow at all. The force acting on them must first overcome a certain resistance, and then the flow may be quite rapid. For this reason in plastic solids the rate of flow is not exactly proportional to the impelling force or the shearing force. On the other hand in truly fluid materials we generally find an exact proportionality between the shearing force and the rate of flow.

So far only one set of observations has been made which might serve as a test to decide whether protoplasm was a true fluid or a plastic solid. In a recent study of the protoplasm of marine eggs (Heilbrunn, 1926a), it has been found that for a certain range of values at least, the rate at which the granules move through the protoplasm is proportional to the shearing force. Hence in this type of protoplasm it is probably true that we are dealing with a fluid rather than with a plastic solid. But it is possible, and indeed even probable, that many other types of protoplasm are plastic solids.

THE ABSOLUTE VISCOSITY OF PROTOPLASM

Most students of the viscosity of protoplasm have been content with comparative values. The viscosity at one time, or under a given set of conditions, is found to be greater or less than at another time or under another set of conditions. Only in a few instances has the absolute viscosity of protoplasm been measured. Table 1 shows these measurements. The viscosity measurements are given in absolute units. Water has an absolute viscosity of approximately 0.01. It is necessary therefore to multiply the figures in the table by 100 in order to obtain the viscosity in terms of that of water.

Not all of the above measurements are equally trustworthy. Seifriz in using the magnetic method introduced nickel balls 16 microns in diameter into egg cells only 150 microns in diameter. Such large foreign objects would almost certainly produce injury.

The measurements show a wide divergence in the viscosity of protoplasm. The material of the sea-urchin and *Cumingia* eggs is relatively fluid. The granules of these eggs are suspended in a liquid with the viscosity of a typical protein solution. The presence of the granules themselves adds to the viscosity of the entire mass. Various authors have suggested formulæ for the calculation of the viscosity of a suspension, if the viscosity of the suspen-

sion medium and the concentration of suspended material is known. Another formula, that of Bingham (1922), requires a knowledge of that concentration of the suspension at which the viscosity becomes infinite. Inasmuch as the concentration of the protoplasmic suspension can be increased by decreasing the volume of the cells, it is possible to determine the concentration of granules at which the protoplasmic viscosity becomes infinite. It is only necessary to shrink the eggs in hypertonic solutions, and by centrifuge tests to determine the exact point at which the viscosity becomes infinite or approaches infinity. Application of the formula of Bingham as well as the formulæ of Einstein and Hatschek shows that the viscosity of the entire mass of the protoplasm of sea-urchin and *Cumingia* eggs is about two or three times that of the fluid between the granules, (see Heilbrunn, 1926c). The marine egg protoplasm and that of the plant cells studied shows a relatively low viscosity. On the other hand the viscosity of *Paramecium* protoplasm is unusually high. In this determination Miss Fetter centrifuged large food vacuoles of known specific gravity and measured their speed of movement through the protoplasm. In such a study the movement of the vacuoles would be greatly retarded by any formed elements in the protoplasm. With our increasing knowledge of the complexity of various Protozoa it is not at all unlikely that such formed elements exist within the *Paramecium* cell and serve to resist the passage of the vacuoles. Rees in his figures of the neuromotor apparatus of *Paramecium* (1922) apparently shows it ramifying into the endoplasm, in which position it would doubtless tend to prevent a passage of the vacuoles of the cell. It would be interesting to determine whether the protoplasm of *Paramecium* behaved as a plastic solid. This could easily be done by centrifuging at different speeds (see above).

TABLE 1

Absolute viscosity measurements

MATERIAL	METHOD	ABSOLUTE VISCOSITY	AUTHORITY
Starch sheath cells of *Vicia faba*, a leguminous plant	Gravity	0.08–∞ Average value 0.24	Heilbronn, 1914
Various species of slime molds just before fruiting	Magnetic	0.09–0.185	Heilbronn, 1922
Eggs of sand dollar, *Echinarachnius*	Magnetic	Slightly less than 8.0	Seifriz, 1924
Sea-urchin eggs, granule free protoplasm	Centrifuge	0.02	Heilbrunn, 1925
Sea-urchin eggs, entire protoplasm	Calculated from previous value	0.04–0.06	Heilbrunn, 1925
Cumingia eggs, granule free protoplasm	Centrifuge	0.04	Heilbrunn, 1925
Cumingia eggs, entire protoplasm	Calculated from previous value	0.12	Heilbrunn, 1925
Paramecium	Centrifuge	80	Fetter, 1925

VISCOSITY CHANGES DURING PROTOPLASMIC ACTIVITY

Life is a succession and a medley of chemical changes. The energy derived from these chemical transformations is what makes vital activity possible. In

recent years the biochemist and the physiologist have had some success in tracing out a few of the many chemical reactions that occur in living matter. These chemical reactions must be related in one way or another to the physical behavior of the protoplasm. Most of the obvious manifestations of life are physical. Movement, the passage of an impulse along a nerve fiber, the division of a cell—all these involve physical mechanism. No amount of knowledge concerning the chemical transformations of protoplasm can in itself solve the riddle of what actually makes a muscle contract or a cell divide. The problem is essentially a physical one.

Living substance is colloidal—it is universally so. The activity of living things is almost certainly bound up with some sort of colloidal change. But what?

One peculiarity of colloids is the fact that they readily undergo changes in their physical state. Fluid one moment, in an instant they may be converted into a more or less rigid mass. Or vice-versa, a semi-solid gel can quickly become transformed into a fluid sol.

Physiologists generally, even before colloid chemistry emerged as a science, have always been ready to assume colloid chemical explanations of vital activities. Thus from the first, most theories of muscular contraction have postulated some sort of colloidal change. And colloidal explanations have been advanced for many other types of biological phenomena. The attempts to prove or disprove these hypotheses have in most cases not been very fortunate. Time and again physiologists have compared protoplasm to this or that inanimate colloid, and as a rule they took these comparisons much too seriously. Often enough biologists have made observations on gelatine in the hope that their results might throw some light on the mysterious behavior of living protoplasm. It is doubtful if there is any colloid more unlike protoplasm in its physical behavior than gelatine. This should have been obvious from the first, for the most striking fact about the behavior of gelatine is that it becomes more fluid as the temperature is raised, whereas protoplasm quite certainly undergoes the reverse sort of change. And this is only one of a great number of essential differences.

The only way to study the colloidal changes of living substance is to observe living substance itself. When the chemical composition and arrangement of living protoplasm become better known than they are at present, it may be possible to find non-living materials which to some extent resemble it in their physical behavior. Even now such studies might be pursued with profit. Most types of protoplasm are concentrated suspensions of visible granules. The colloid chemist has studied such concentrated suspensions very little, in spite of the fact that the small amount of work already done has indicated that the subject is one of great interest. If comparisons between protoplasm and non-living matter are to be made at all, it would doubtless be much wiser to compare protoplasm with types of material which in some degree resemble it. But after all, until the day comes, if it ever does, when we can actually synthesize living protoplasm, no inanimate material can be expected to show exactly the same colloidal behavior as protoplasm. If we are to really be sure of the colloidal changes of protoplasm we must study them directly.

In making observations on living cells, the most reliable index of colloidal change is the viscosity. In colloidal systems, when a sol changes to a gel, it assumes form and is as a result elastic; at the same time its viscosity undergoes a decided increase. No one has as yet made a proper study of the elasticity of cell protoplasm,

but as has been pointed out, the viscosity can be measured in a variety of ways. As a matter of fact the colloid chemist has often used viscosity change as an index of gelation. Thus to quote a leading authority, "The viscosity is the property which changes most strikingly during the sol-gel transformation, and hence has been investigated most closely" (Freundlich, 1926).

In a way it is rather difficult to compare observations on non-living and living systems. The terminology of colloid chemistry has been built around a study of colloids in test tubes. In a cell, conditions are different. Thus although it would probably be correct to say that any pronounced increase in the viscosity of protoplasm indicated that the protoplasm was a gel, it should be noted that increases in the viscosity of protoplasm might really be due to a variety of causes. In a test tube precipitation phenomena lead to a settling out of the precipitate with a consequent decrease in the viscosity of the remainder of liquid. But when substances are precipitated out of the protoplasm of the cell, they remain within the extremely narrow confines of the cell itself, and the viscosity of the entire protoplasm is increased. Changes in the viscosity of protoplasm might also be due to changes in the surface properties of the granules suspended within the cell, as well as to changes in the material between the granules. For a more complete discussion of this point see Heilbrunn (1926b). In the future it will not be enough to discover that protoplasmic viscosity increases and that the protoplasm becomes a gel, the question will be asked as to the nature of the changes that brought about the increase in viscosity.

Viscosity change during vital activity has been studied most in marine eggs. In a paper published in 1915 (Heilbrunn, the sea-urchin egg is accompanied by a sharp increase in viscosity and this observation has been generally accepted. Centrifuge tests show the difference in viscosity very markedly. With the same amount of centrifugal treatment unfertilized eggs show far more granular movement than do eggs fertilized fifteen or twenty minutes previously (at about 20°C.). Fatty granules or oil droplets move to one pole of the egg, colorless granules and pigment granules move to the opposite pole of the unfertilized eggs. In the eggs centrifuged for the same length of time and at the same speed twenty minutes after fertilization, there is no visible movement of granules at all. The difference is striking.

If sea-urchin eggs are centrifuged two or three minutes after insemination, the colorless granules of the egg move just as rapidly as before fertilization. On the other hand, not all the pigment granules are moved by the centrifugal force. In the cortex of the fertilized egg there is a larger number of pigment granules which have resisted the centrifugal force, than there are in similarly treated unfertilized eggs. This observation may be due either to the fact that at fertilization the pigment granules move out into the cortex of the egg where they become attached to the outer membrane and resist the centrifugal force or it may be due to the fact that after fertilization there is a cortical gelation or coagulation. Miss Hyman's experiments favor the latter interpretation (1923).

In a preliminary note published in 1917, and in the complete paper published in 1920 (Heilbrunn, 1917, 1920a), the viscosity changes during the cell division of the sea-urchin egg were described in detail. These results were later made more exact for the moment or two before cleavage (Heilbrunn, 1921).

was being done and in the same laboratory, Chambers was making estimates of viscosity changes during cell division in the sea-urchin egg, using the microdissection method (Chambers, 1917b, 1919). Although at first sight his results might be thought to agree with those arrived at by the centrifuge method, they really differ in one or two important points. Some time later Seifriz (1920) also published a few estimates of protoplasmic viscosity during cell division.

From the published descriptions of Chambers and Seifriz it is not easy to picture the changes they believe to occur. This is in part due to the fact that Chambers frequently refers to various stages in terms of minutes following fertilization or minutes before cleavage, although obviously the number of minutes which elapse before a certain stage is reached is a function of the temperature. For the sake of clearness therefore it was thought worth while to plot Chambers' results, even though only the roughest sort of a curve could be obtained. In order to be certain to cite the facts as Chambers describes them, a condensed account in the words of the observer is here given. Quotations are from the 1919 paper.

> Immediately after fertilization the cytoplasmic granules readily flow by the moving needle. (This is taken to indicate low viscosity.) . . . . When the sperm aster is at its full development the highly viscous state of the cytoplasm is detected by the needle. . . . . This condition is at its height 10 to 15 minutes after fertilization. Fifteen to 20 minutes after fertilization, the radiations of the aster begin to fade from view, with a reversal in the cytoplasm of the semi-fluid to a more fluid state. . . . . Toward the end of this stage, which lasts for about 20 to 30 minutes. . . . . Shortly before cleavage, about 40 to 50 minutes after fertilization, an increase in firmness sets in. . . . . The time of appearance of the amphiaster until completion of cleavage lasts from 10 to 15 minutes. The increased viscosity of the egg during this amphiaster stage. . . . . After the completion of the cleavage process, there are indications that the firmness of the cytoplasm persists.

The account given in the 1917 paper does not agree absolutely with this account. After the amphiaster has formed, and shortly before cleavage, Chambers in 1917 is led to conclude from granular movements near the equator of the nuclear body, that a liquefaction occurs, at least in this region of the cell. But he says, "I was not able to convince myself on this point by the use of the needle."

Figure 1 shows the results obtained by the centrifuge method and those of Chambers on the viscosity of the sea-urchin egg during the period between fertilization and cleavage. The centrifuge data are for the most part those published in 1920, and are based on a number of observations. The viscosity changes shown by the centrifuge are represented by an unbroken line. Chambers' data are approximated by the line of dashes. Both curves show an increase in viscosity followed by a decrease. The outstanding difference is that Chambers regards the period during which the amphiaster is fully formed as a period of increased viscosity, whereas centrifuge tests show it to be a stage of low viscosity. Seifriz's microdissection estimates agree with the centrifuge tests in regarding the amphiaster stage as one of lowered viscosity. Thus he states (1920),

> With the first appearance of the amphiasters there is a pronounced decrease in viscosity of the central region of the cell, and this condition is maintained throughout the intermediate stages of division (from middle prophase to late anaphase).

In figure 1, the total time between insemination and cleavage is taken as fifty minutes. When the actual time was greater or less than fifty minutes a correction was made for all points plotted.

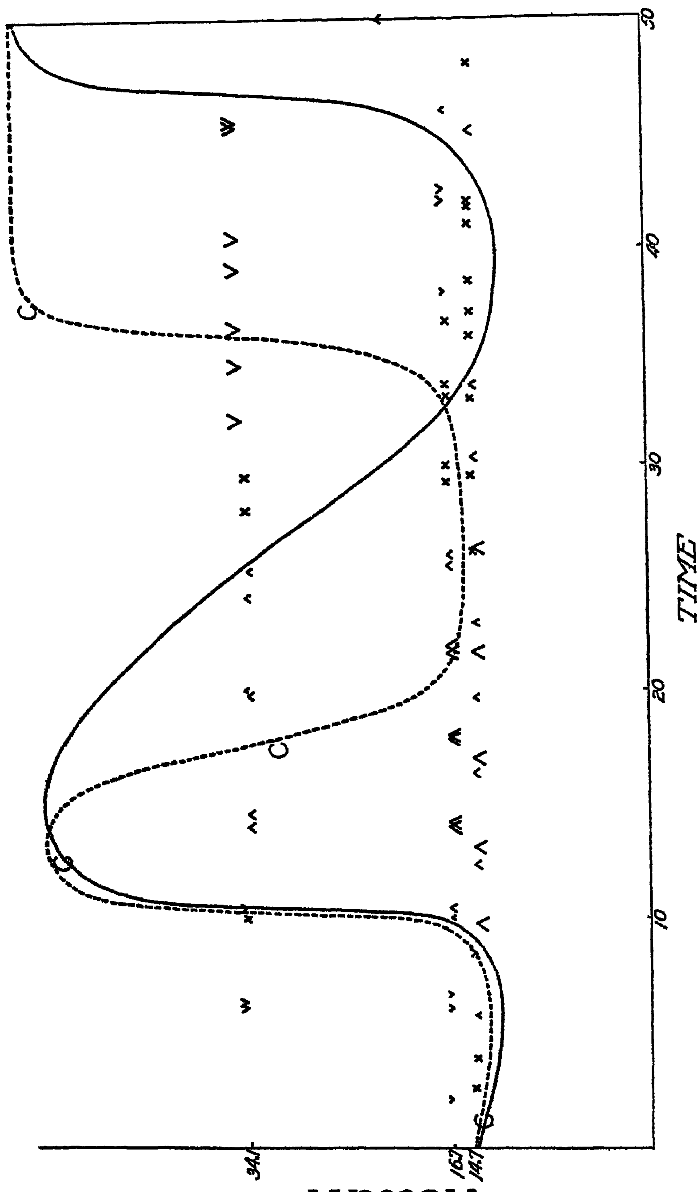

FIG. 1. VISCOSITY CHANGES DURING MITOSIS IN THE SEA-URCHIN EGG. THE UNBROKEN LINE IS PLOTTED FROM THE CENTRIFUGE DATA (HEILBRUNN), THE DOTTED LINE IS A ROUGH ESTIMATE BASED ON THE MICRODISSECTION EXPERIMENTS OF CHAMBERS

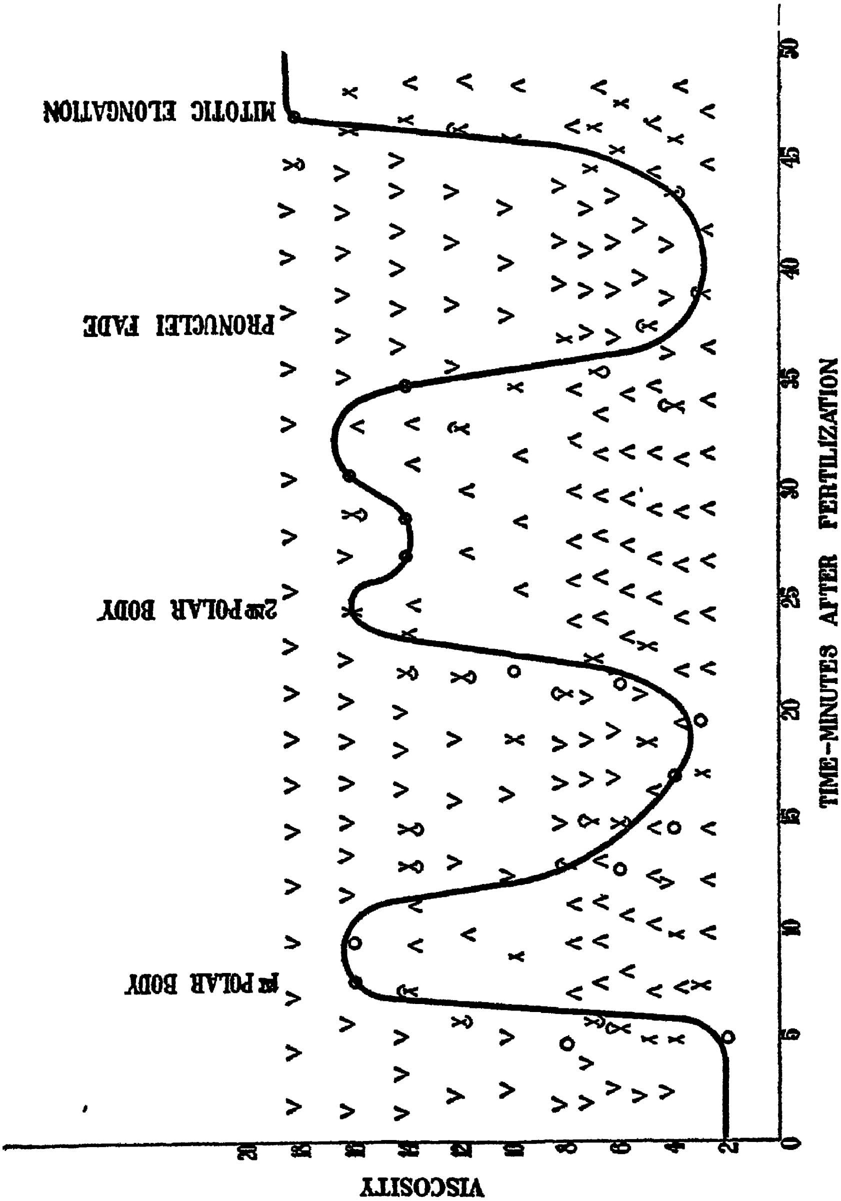

FIG. 2. VISCOSITY CHANGES IN THE PROTOPLASM OF CUMINGIA EGGS DURING THE INTERVAL BETWEEN FERTILIZATION AND THE FIRST CLEAVAGE

The ordinates represent arbitrary units of viscosity. When the protoplasm is most fluid it has a viscosity equal to that of the unfertilized egg. Thus it is approximately twice that of water if the granules are disregarded, or four to six times water if the granules are included (see above). In the figure the *V*'s indicate a viscosity less than the value for y at that point, the inverted *V*'s indicate a greater viscosity. The length of the *V*'s and inverted *V*'s is also significant. Points on Chambers' curve are indicated by *C*'s.

The cycle of viscosity changes during the period between fertilization and cleavage in the sea-urchin egg has frequently been confirmed by workers at Woods Hole who have used the centrifuge. As a matter of fact for a number of years classes in the Physiology Course at the Marine Biological Laboratory have duplicated the results outlined above.

With the egg of *Cumingia* it is possible to obtain more exact data concerning the viscosity changes during mitosis. This egg is in the metaphase stage of the first polar body division when it is shed into the sea-water. At this time the egg protoplasm is highly fluid. The viscosity increases just before the completion of the first maturation division, drops again as the second polar spindle develops, rises as the second polar body is given off, to decrease again with the appearance of the amphiaster of the cleavage spindle. The complete curve of the viscosity changes in the *Cumingia* egg is given in figure 2, which is taken from a paper published in 1921 (Heilbrunn, 1921). In this graph, the *X* axis represents time in minutes after fertilization, the total time being fifty minutes. This was regarded as a standard time interval, and observations made on eggs which required a longer or a shorter time for the period between fertilization and cleavage were plotted by making a correction in the time. Thus if the cleavage time for a lot of eggs was sixty minutes instead of fifty, each observation on this lot of eggs was assumed to take place at five-sixths the number of minutes after fertilization at which it actually did occur. The ordinates in figure 2 are arbitrary viscosity units. As a matter of fact, as has been shown by more recent work, they do really represent a fairly close agreement with the absolute viscosity units in terms of water. Each of the symbols of the figure represents a centrifuge test. The *V's* indicate that the viscosity was less than the value of *y* at that point, the inverted *V's* indicate that it was greater. For further details regarding the meaning of the symbols used the reader is referred to the original paper.

The viscosity changes in the egg of *Cumingia* are very striking. The protoplasmic viscosity increases at least five or six hundred per cent in a very short time. The egg of the sea-urchin *Arbacia* is somewhat larger than the egg of *Cumingia*. Its viscosity changs are not as pronounced as those of the latter, the viscosity increase probably not being more than three or four hundred per cent. The egg of *Nereis* is larger still and contains a larger proportion of yolk materials, and a relatively small spindle. In this egg the viscosity changes are to some extent obscured and are rather more difficult to follow. However the same cycle of viscosity changes was found to occur. It is apparent that with the increase in the size of an egg and the relative decrease in the size of the spindle in proportion to the total mass of the cell, the viscosity changes during mitosis become less evident. But even in an egg as large as the frog egg, Ödquist (1922) has been able with the centrifuge to detect periodic variations in the viscosity of the proto-

plasm. These he regards as in essential agreement with my results on *Cumingia* and *Arbacia* eggs.

It is interesting to find moreover that exactly the same sort of cycle of viscosity change during mitosis occurs in a widely different type of cell. Thus Zimmermann (1923) in the alga *Sphacelaria fusca* was able fully to duplicate the results obtained with *Arbacia* and *Cumingia* eggs. He states,

> Wir können also in der Prophase eine Zunahme der Plasma-Viskosität beobachten, in der Metaphase eine rasche Abnahme und nachher wieder eine allmähliche Steigerung. Die Versuche stimmen überein mit Zentrifugierungsversuchen, die amerikanische Forscher, u. a. Heilbrunn (1920), an tierischen Zellen unternommen haben und ferner mit meinen Beobachtungen über die Brownsche Bewegung.

Zimmermann used the centrifuge method.

The periodic cycle of viscosity change during cell division is almost certainly related to the rhythmic changes in susceptibility of dividing cells to various toxic substances. Such rhythmic changes in susceptibility were described by Lyon many years ago (1902, 1904), and they have been interpreted by many biologists as indicating a rhythmic change in the permeability of the cell during mitosis. But the cell is not only periodically more and less susceptible to chemical substances, it also goes through a cycle in which it is more and less susceptible to cold, to heat, and to light (Schleip, 1923; Ruppert, 1924). Such rhythmic susceptibility to physical agents can scarcely be interpreted on the basis of a periodic change in the permeability of the plasma membrane of the cell, for the changes in permeability could scarcely affect the entrance of heat or light. As a matter of fact there is no valid reason for associating the cycle of susceptibility changes with an almost purely hypothetical cycle of permeability changes, especially inasmuch as the actual facts regarding viscosity change offer just as simple an explanation.

There is strong evidence that the viscosity changes which occur during cell division in the sea-urchin egg are an essential part of the process. This has been clearly shown by the author's work on artificial parthenogenesis (1915, 1925a). Of the many different types of treatment which are capable of inciting the egg to divide, each and every one produces an increased viscosity in the protoplasm. There are no exceptions. Moreover, it is only necessary to prevent viscosity change in order to prevent mitosis from occurring (Heilbrunn, 1920a and b). Such prevention of viscosity change need not produce any decided injury in the protoplasm, the egg is anesthetized. A fuller discussion of the subject of anesthesia will be given in the next section. At this point it is only necessary to state that no matter how viscosity change is prevented, the mitotic phenonena are always inhibited.

It has thus been demonstrated not only that viscosity changes occur during mitosis, but that these changes are important and must be considered in any theoretical interpretation of the process. It is undoubtedly true that viscosity changes occur in the course of other vital phenonena, but in no case is the evidence as complete as it is in the case of cell division.

In 1919, Leblond (1919 a and b) published observations on viscosity changes in freshwater algæ. He studied the Brownian movement in the protoplasm of these cells, and he concluded that the protoplasm might change from a gel to a sol, and back again. Leblond states that the gel-sol transformation occurs only when the alga cell changes from a period of rest to a period of functional activity such as growth, division, or reproduction. A similar change is found in various

marine ova. In the primary oocytes of various forms, such as *Nereis* for example, the protoplasm is quite rigid. The breakdown of the germinal vesicle introduces a period of activity and the protoplasm becomes much more fluid.

In *Amœba*, Bayliss (1920) showed that electrical stimulation produced a cessation of Brownian movement. This he interpreted as being the result of a gelation in the protoplasm.

An interesting case has recently been described by Weber (1925d). From a study of the plasmolytic behavior of the guard cells of the stomata of *Vicia faba*, he concludes that the viscosity of the outer layer of the protoplasm of these cells is high when the stomata are open and low when they are closed.

One of the most interesting questions in the whole field of physiology is the question as to the nature of the physical changes that occur when a muscle contracts. In the past some physiologists have held the view that a muscle is coagulated or gelated during activity, others have fought for the opposite theory and have regarded muscular contraction as being primarily due to the swelling of a gel. Recently Gasser and Hill (1924) have attempted to determine which type of viscosity change actually does occur when a muscle contracts. Attaching a muscle to a steel spring, they have studied the effect of the muscle in damping the vibrations of the spring, and from this have calculated the viscosity. They conclude that the viscosity of the muscle increases markedly during contraction, but unfortunately there seems to be a question as to whether their results might not be open to some other interpretation.

It is obvious that the work on the viscosity changes during protoplasmic activity has just begun. In the future, and probably in the near future, many other types of cells will be studied in the hope of finding some correlation between the colloidal behavior of the protoplasm and its vital behavior. Furthermore, study will be directed toward a better understanding of the sequence of chemical and physical phenomena which are involved in viscosity change.

VISCOSITY CHANGES DURING ANESTHESIA

It has already been stated that the viscosity changes in protoplasm are closely related to at least some of its important functions. No better proof of this statement could be given than some of the recent knowledge regarding anesthesia.

In the first place it should be pointed out that certain anesthetics are almost universal. A low percentage of ether will stop various types of cellular activity throughout almost the whole breadth of the animal kingdom. From this extremely important fact it may be concluded with some show of reason that the essential mechanics of protoplasmic activity are similar in widely different types of the living substance. Ether, in much the same concentration, will stop the movements of a cœlenterate, will prevent the division of a sea-urchin egg, block the passage of an impulse along a nerve, or prevent the contraction of a muscle. It thus is capable of inhibiting many types of physical activity of protoplasm, although apparently it has less influence on the chemical activity of the cell.

What is the nature of the ether effect? Some authors have supposed that the primary action was on the permeability of the plasma membrane, although there has never been an agreement as to whether ether caused an increase or a decrease of permeability. As a matter of fact, most of the evidence as to the relation of ether to permeability is untrustworthy (Heilbrunn, 1925c).

It was shown by Heilbrunn in 1920 that ether and various other fat solvents when present in dilute concentration lower the viscosity of sea-urchin egg protoplasm. In higher concentration they cause an irreversible gelation and death. In plant cells as well as in animal cells, dilute ether solutions cause a decrease in protoplasmic viscosity, whereas more concentrated solutions produce an increase (Heilbronn, 1914, 1922; Weber, 1921b, 1925b). This is true for cells of *Vicia faba*, for slime molds, for *Spirogyra* cells, for cells of the leaf of *Elodea*, and the stalk of *Callisia repens*. In the case of the sea-urchin eggs ether and other fat solvents act as anesthetics only when they lower the viscosity. Weber also favors the view that the concentrations of ether which lower viscosity are the anesthetic concentrations for plant cells. Certainly they would inhibit cell division. On the other hand a decrease in viscosity, or in other words a heightened fluidity, could scarcely be expected to prevent protoplasmic streaming. This is prevented by higher concentrations of ether, concentrations great enough to produce gelation. The only difference between plant and animal protoplasm lies in the fact that in the sea-urchin egg the gelation produced by ether is irreversible, whereas it is reversible in at least certain types of plant cells. This perhaps may find an interpretation in the fact now being presented in another paper (Heilbrunn, 1927) that ether in higher concentrations causes a peculiar reaction in the interior of sea-urchin protoplasm, a reaction which depends on the formation of numerous surface films in the interior of the cell.

The actual amount of the viscosity lowering in sea-urchin egg protoplasm has been measured more or less quantitatively (Heilbrunn, 1925c). In unfertilized eggs 2.5 per cent ether lowers the viscosity to about a half of its original value. In fertilized eggs, there is an even more pronounced effect, the viscosity being reduced to one-sixth or one-eighth of its original value.

If we assume that all physical activity of protoplasm is related to colloidal change, then it might be possible to prevent activity either by preserving a state of low viscosity or by preserving a state of high viscosity. It is indeed quite probable that there are two main types of anesthesia. In the one type the protoplasm is kept in a highly fluid condition, in the other it is held in the state of a gel. These two types of anesthesia can actually be demonstrated in the sea-urchin egg (Heilbrunn, 1920b).

EFFECT OF TEMPERATURE ON PROTOPLASMIC VISCOSITY

In a paper published in 1913, Fauré-Fremiet published viscosity measurements of *Ascaris* protoplasm at different temperatures. Fauré-Fremiet's paper is over three hundred pages long and he does not mention his viscosity experiments in his table of contents or summary. It is not surprising therefore that this paper has been generally overlooked by later workers in the same field. The optimal temperature of *Ascaris* protoplasm is close to 35°C.; as the temperature drops below 35°, the viscosity of the protoplasm progressively increases. Fauré-Fremiet measured the viscosity by noting the length of time necessary for displacement of mitochondria granules when the eggs were centrifuged. He records only five observations. These are shown in the following table, in which the second column gives the time necessary at a centrifugal speed of 2500 turns per minute to throw the mitochondria from one end of the cell to the other.

Temperature	*Time*
35°C.	4 minutes
30°	8 minutes
23°	20 minutes
18°	45 minutes
8°	225 minutes

It will be noted that there is no measurement between 18° and 8°C.

In 1917, F. and G. Weber determined the viscosity of the protoplasm of the cells of bean seedlings (*Phaseolus multiflorus*) by the gravity method. They found that the viscosity increased as the temperature was lowered.

Pantin (1924) found by centrifuging the eggs of *Nereis* at different temperatures that the viscosity decreased as the temperature was raised. He made measurements at only four temperatures, 0°, 10°, 20°, and 30°C.

In 1924, I plotted the temperature viscosity curve for the protoplasm of the *Cumingia* egg. The viscosity is relatively very high at 1°C. But at 2°C. the viscosity of the protoplasm drops to a low value, rising then gradually as the temperature is raised until it reaches a maximum point at about 15°C. At temperatures above 15°C. the viscosity again decreases progressively, until suddenly at about 32°C. a sharp increase in viscosity occurs. Heilbronn (1922) in his study of slime mold protoplasm also found a maximum in viscosity at about 15°C. Both above and below this temperature the viscosity of the protoplasm decreased.

It is possible that such a maximum escaped other workers who failed to make observations at frequent temperature intervals. If one compares the data obtained by Pantin on the *Nereis* egg with the viscosity curve plotted for *Cumingia*, it will be found that three out of the four points determined by Pantin fit very well on the curve as plotted for *Cumingia*, and the fourth point is not so very far off. However there is good reason to suppose that there may be an essential difference between the protoplasm of *Nereis* and *Cumingia*. In the form of *Nereis* obtainable at Woods Hole, the unfertilized egg has a large germinal vesicle and its protoplasm is relatively very viscous, that is to say it is a gel, whereas the protoplasm of *Cumingia* is highly fluid.

In his comment on the viscosity curve in *Cumingia* eggs, Pantin states that

> The curves showing the relation of the majority of biological processes to temperature show no relation to such a viscosity temperature curve. For instance, the curve relating temperature to the rate of beat of the Terrapin heart is a smooth curve gradually reaching zero near 0°C.; if the state of the protoplasm changed with the temperature, as in Cumingia eggs, one would expect the change to be reflected by a deviation from the observed smooth curve, the deviation being maximal where the viscosity was maximal.

As a matter of fact in many cases such deviations do occur at about 15°C. (see Kanitz, 1915). This point has recently been emphasized by Crozier (1924).

EFFECT OF ELECTRIC CURRENT

It has already been pointed out that when an electric current is passed through an ameba, the viscosity of the protoplasm increases (Bayliss, 1921). Bersa and Weber (1922) found for cells of *Phaseolus* that small electric currents caused a sharp increase in viscosity. They determined the viscosity change with the centrifuge method and found it to be at least threefold. When the electric current stopped flowing, the protoplasm returned nearly or completely to its original fluidity.

EFFECT OF X-RAY AND RADIUM

Weber (1923) found no effect of X-ray on the protoplasmic viscosity of two types of plant protoplasm. He radiated *Spirogyra* with 170 "H" units, and then cen-

trifuged five minutes later. There was no observable difference between the radiated material and the controls. Another test twenty hours after the radiation showed an increased viscosity in the treated cells. This Weber interprets as being due to a secondary effect. Weber also radiated seedlings of *Phaseolus multiflorus* with 24 H units. Following such treatment there was no observable change in the protoplasmic viscosity.

Forbes and Thacher (1925) exposed fertilized *Nereis* eggs to radium and found a slight decrease in protoplasmic viscosity. They used the centrifuge method.

THE ACTION OF VARIOUS CHEMICALS

The action of fat solvent anesthetics has already been considered. Various types of protoplasm have their viscosity lowered by weak concentrations of fat solvents. Higher concentrations produce gelation.

Apparently all substances which have a marked effect on the life of the cell produce decided changes in protoplasmic viscosity. All living cells require the presence of salts for their existence. Life doubtless began in the ocean and all forms of protoplasm have a close relation to the salts of their environment. Long ago physiologists showed that these must be properly balanced. Sodium or potassium chloride alone is usually toxic, calcium chloride alone is likewise toxic. Only a combination of sodium or potassium chloride on the one hand and calcium or magnesium chloride on the other gives conditions favorable for life. Doubtless the specific effects of these various salts are many. One important effect is their influence on the viscosity.

In 1923 I showed that in sea-urchin eggs and in *Stentor* sodium chloride tends to increase the viscosity of the interior protoplasm. Magnesium and calcium chloride have the opposite effect. Similar results have apparently been obtained by Scarth for plant protoplasm (Scarth, 1924b). After long exposures to calcium the initial liquefaction may change to a coagulation (see Heilbrunn, 1925b). Aluminum acts like calcium but much more powerfully. Experiments with calcium are complicated by the fact that this salt plays a specific rôle in the surface precipitation reaction (Heilbrunn, 1927).

Both acids and alkalies coagulate protoplasm, at any rate they cause a pronounced increase in the viscosity. The effect of carbon dioxide has been studied by Jacobs (1922). He used the centrifuge method, and studied the effect of bubbling carbon dioxide through the surrounding medium on the protoplasmic viscosity. In protozoan cells, *Paramecium* and *Colpidium*, he found that short exposure to carbon dioxide caused liquefaction, whereas longer exposure caused coagulation. Jacobs also experimented with sea-urchin eggs, and with this material he found only coagulation. However, as he himself points out, his experiments with sea-urchin eggs are very few in number. In occasional experiments with sea-urchin eggs I have found that their behavior is not unlike that of the protozoan cells.

Finally it may be pointed out that many protoplasmic poisons cause gelation in protoplasm. Copper sulphate, mercuric chloride, formalin and various other poisons have been tested on sea-urchin eggs. All of them produce a rapid and complete gelation.

The present review of the literature on protoplasmic viscosity has been hastily prepared. It was written at the request of the editor of this journal more or less against the writer's better judgment. It is his hope that the survey of literature

which he has presented has not been too incomplete. There is indeed no claim for completeness. The literature on the viscosity of protoplasm is widely scattered, and some of it has doubtless been overlooked.

In preparing the review it was felt worth while to stress the work which in the sober judgment of the writer gave indication of being accurate. Physical measurements in biology, at least in the study of protoplasm, are of comparatively recent date. The average biologist is scarcely trained in their evaluation. He is apt to weigh equally the statements of a worker who estimates viscosity by looking at a cell with those of other workers who make an honest effort to obtain reliable objective measurements. In whatever criticisms he has made the author has been actuated solely by one motive, namely that of discovering the truth in so far as possible.

In the future the physical study of protoplasm, if it is to prosper, must be conducted by workers who are willing to submit both their own work and that of others to close scrutiny and criticism. Accurate measurements of the physical properties of living matter are not easy to make. There are numerous pitfalls for the incautious seeker after quick discoveries. Only by a proper realization of the difficulties and a willingness to face them can progress be made.

The fact that within the last ten or twelve years a real beginning has been made is decidedly encouraging. We now know a considerable number of definite, well established facts in regard to the viscosity changes which may occur in living matter. It is in the hope that a review of what is now known may help in the accumulation of additional and more accurate data, that this material is herewith presented.

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ABNORMAL SEXUALITY IN ANIMALS

II. PHYSIOLOGICAL

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IN A previous issue of this Journal (Vol. I, No. 3, July 1926, pp. 315–359), there was discussed Abnormal Sexuality, I. Intersexuality; A. Due to disharmony in the distribution of the genotype; B. Due to disharmony in the composition of the genotype. The subject is continued herein.

C. *Intersexuality due to the overriding of the genotype*

For purposes of discussion, it is proposed to refer to this category as physiological intersexuality. In certain of the cases cited as examples, there must remain a doubt as to which of these arbitrarily chosen classes, genotypical and physiological, the particular example belongs until more is known of the genetics of the form, and of the mechanism concerned in the processes of developmental physiology. It is solely in order to ease discussion that this legitimate rigid classification has been adopted.

1. Through the action of a foreign biochemical agency. (a) The case of the bovine free-martin. Twins are not uncommon in cattle. They may be two perfectly normal males, two normal females, one male and one female, both normal, or one normal male and an individual which is abnormal in its sex organization, and in this alone. The questions to be considered are these: (1) Are twins in cattle identical or fraternal, i.e., do they have their origin in one and the same zygote or in two separately fertilized ova? If they are identical, then the sexually abnormal individual must be a genotypic male, i.e., of the same sex as its normal co-twin; if the twins are fraternal, then the abnormal individual may be either male or female, genotypically. (2) How is this abnormality produced?

The earlier investigators who had examined the case of the bovine free-martin had regarded the abnormal individual as an identical twin, and, therefore, as a genotypic male (Spiegelberg, Hart, Bateson, and Cole). However, in all save one of 126 cases of twins in cattle thoroughly examined by Lillie, two *corpora lutea* were found. The inference is that twins are almost invariably binovular in this animal, since two ova are concerned in such pregnancies; for when an ovum is discharged from the mammalian ovary, the scar tissue of the ruptured follicle remains as a glandular structure known as the *corpus luteum*.

The two fertilized ova pass into the bicornuate uterus and become attached to the uterine mucosa. As the zygotes increase in size, the embryonic membranes of the two fetuses meet to adhere and in many cases to fuse. If such fusion occurs, an anastomosis (intermingling) of their blood vessels can result, so that a common vascular intercommunication may become established.

Thus the situation arises in which the sex-hormone of each developing individual is at liberty to pass into the tissues of its co-twin. The sex-hormone is the instrument which models the sex organization alone. The internal secretions of the pituitary, thyroid, adrenal, and so forth, can also pass from each individual to the other, but these are mainly concerned in the general and not in the special development of the individual and will be alike in both twins.

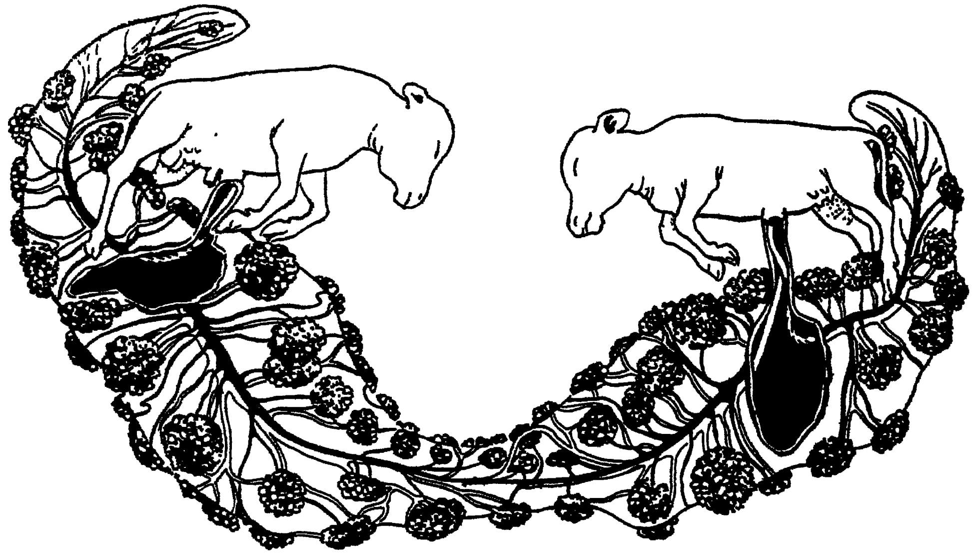

FIG. 15. THE BOVINE FREE-MARTIN (AFTER LILLIE)

But if it so happens that the twins are bisexual (and a study of the sex-ratio in cattle shows that by the laws of probability three possible sex combinations in twinning must occur in the proportion of 1♂♂ : 2♂♀ : 1♀♀, and that the twin combination that includes a free-martin must be regarded as male : female), and if fusion of the chorions occurs, and further if a vascular intercommunication becomes established, as it does in seven cases out of eight, the sex-differentiation of both individuals will be directed by that sex-hormone which is exhibited earlier or which is more potent. The testis becomes differentiated at an earlier stage of development than the ovary, and so the sex-hormone of the male is liberated before that of the female. The male sex-hormone is liberated before the embryonic gonads of the genotypic female have undergone differentiation into ovaries; such differentiation is prevented and so there is no question of a competitive action between male and female sex-hormones. The female twin (i.e., genotypic female) will thus pursue her sex-differentiation under the direction of the male sex-hormone of her co-twin and will, therefore, come to possess more or less completely the organization of the male. The assumption of the male characters in the case of the fetuses examined is imperfect; the external genitalia are of the female pattern, the internal organs of reproduction more or less completely male. The end-result will have a relation to the time of exhibition of, and to the efficiency of, the male sex-hormone. The variation in the size of the testes of the male co-twin

and of the extent of vascular intercommunication seems to point to the conclusion that the amount of the hormone is not a significant factor in the production of a free-martin but that there is a minimum stimulus and the reaction is of the "all-or-none" type. It is seen that the tissues of the genotypic male respond completely to the stimulus of the testicular sex-hormone, whereas those of the genotypic female fail to do so. Now it is known that genotypic male and female tissues are to be distinguished by differences in their chromosome content, and it is reasonable to assume that because of these differences they differ also in their physiological constitution. It is probable, therefore, that though both kinds may be capable of responding to the stimulus of one and the same sex-hormone, they will respond differentially. The male co-twin develops testes because he is a genotypic male and becomes a phenotypic male because he develops testes. His embryonic gonads became testes because their differentiation was pursued under the direction of the male-differentiating reactions elaborated by the interaction of the genes in the sex-determining gene complex. The sex-hormone elaborated by the testes, passing into the body of the genotypic female, swings her sexual differentiation in the male direction, but the swing is not complete, because the sex-hormone of the testis is not equivalent physiologically to the male-differentiating substances elaborated by the sex-determining factors, and because her tissues are constitutionally different from those of the genotypic male. The degree of development of the mammary glands of the free-martin is as that of the immature female. This fact is not without interest for it is known that mammary development is not an infallible indication of the presence of ovarian tissue: in the human subject many cases of considerable development of the mammæ in the male have been recorded. It is to be noted that in the case of twinning involving one normal male and one normal female, there is no vascular anastomosis.

Moore (1921) has shown that it is possible in the rat to remove one testis and replace it by an ovary and that following this, both testis and ovary continue to produce functional gametes. It is possible, therefore, to secure a balance of the male and female hormones in one and the same individual and so to produce an artificial hermaphrodite although such an individual could not function both as a male and a female. Sand (1923) has demonstrated the effects of simultaneous implantation of ovary and testis into an infantile castrated guinea pig and of implantation of ovaries into the testes of rats and guinea pigs and has shown that artificial hermaphroditism with pronounced bisexuality of the psycho-sexual characters could be produced associated with the synchronous development of both male and female sexual organs. These observations support the suggestion that in the free-martin there is no antagonism of sex-hormones, but that the male sex-hormone is liberated first and inhibits the proper development of the ovary. As has been stated, intersexuality is comparatively common in the goat and the pig. It is probable that many of these cases are free-martins, for Keller (1920) and Hughes (1927) have shown that the same kind of placental anastomosis can be demonstrated.

That this is the correct interpretation of the case of the free-martin seemed to be supported by the work of Minoura (1921), who claimed to have produced an equivalent condition in the chick. A small window was made in the shell of a seven to nine days' incubated fertile hen's egg,

and on to the vascular area of the chorio-allantoic membrane were grafted small pieces of testis or of ovary from embryo chicks and adult fowls. In a certain proportion of cases the operation did not interfere with the further development of the chicks and the grafts, it was claimed, showed modification in their sex organization; fourteen individuals were affected as a result of ovarian grafts and sixteen by testicular. In the case of male embryos which had received an ovarian graft, modification in the direction of the female condition was seen, the right testis being smaller than the left (in the female the right gonad atrophies and disappears), while the Müllerian ducts persisted instead of atrophying as in the normal male. In females grafted with testicular tissue, the right and left ovaries were equally developed and the male genital ducts persisted. In this way, Minoura claimed to have produced "free-martins" of both sexes. If this be so, then the mechanism of sex-differentiation in birds would appear to be identical with that in mammals, the critical point being the differentiation of a gonad of one or the other type which proceeds to elaborate a specific internal secretion. It is not clear, however, whether Minoura's results might not have been due to a simple retardation of sex-differentiation by operative interference. Anyone who is well acquainted with chick embryology knows that there is a very great variation in the processes of sex-differentiation. Moreover, Greenwood (1925), and also Kemp (1925), repeating this work even more critically and more extensively, have completely failed to confirm Minoura's conclusions.

It is seen that in the mammal the most distinctive sex-dimorphic characters are the secondary gonadic and for the development and maintenance of these the presence and action of functional gonadic tissue is necessary. The physiological action of gonadic tissues of the opposite sex causes the further development of incompletely differentiated structures to follow the direction appropriate to that sex and so far as is morphogenetically possible, renders the individual intersexual. These conclusions are fully supported by the results of experimental intersexuality (Steinach, 1913; Sand, 1923; and Moore, 1919).

All the results of experimental embryology indicate that in the differentiation of the sex-equipment two phenomena are to be distinguished, (1) the development of the embryonic architecture, (2) the differentiation of the component structures during further growth, and the attainment of specific form under the direction of the physiological action of the "hormones." The timely production of these hormones is to be regarded as the function of the genes resident in the chromosomes. In the insect (and physiologically similar forms) the products of metabolism that guide the development of tissues towards definite form and structure are present within the individual cell and are elaborated there almost if not completely independently of the rest of the body. In the mammal the control of differentiation is removed from the genotype of the individual cell to become the especial function of the glands of internal secretion. Intersexuality in the insect is the direct expression of an unusual genotype, in the mammal the genotype can be overridden.

The fecund tortoiseshell tom-cat is indeed a rarity, and many have been the attempted interpretations of this undoubted fact. Little (1920) and Doncaster (1920) have each suggested that the infecund tortoiseshell tom is a feline free-martin, but Bamber (1922) who examined

a series of multiple births, found no indication of chorionic fusion or of intervascular communication.

(*b*) *The reciprocal free-martin in the oppossum.* Hartman and League (1925) described a sex-intergrade opossum which was bought in as a male, for so it appeared, but which was found, on closer inspection, to have skin folds, simultating a pouch, better developed than in the normal male. The penis was of normal size and structure, and the scrotum was well formed but empty; the head, previously described as being of the female type by Hartman, was of the male type. The internal genitalia consisted of an accessory sexual apparatus of the infantile female type. All the parts of the Müllerian duct were present as also were the vagina, lateral vaginal canals, uteri, and Fallopian tubes. The glands were infantile in dimensions and in structure. The round ligaments were normal, and therefore large in proportion to the rest. There were no vasa deferentia and the Wolffian duct derivatives were absent. The gonads were in the position of the ovaries and were very small; their histological structure was somewhat indefinite.

Though the authors could not finally establish their contention that this abnormal individual was a male rendered abnormal whilst in utero by the action of the sex-hormone of a normal female co-twin, they present certain evidence in favor of this interpretation. They compare the specimen with the bovine free-martin, so:

Free-martin	*Specimen*
Genotypic female.	
Female habitus.	Male habitus.
Female external genitalia.	Male external genitalia.
Udder present.	Pouch present, but defective.
No scrotum.	Scrotum.
Clitoris.	Penis.
Müllerian duct repressed.	Müllerian duct developed.
Wolffian duct developed.	Wolffian duct inhibited.
Male vas.	Gärtner's duct only.
Inguinal ligaments.	Round ligaments.
Gonad more like testis.	Gonad more like ovary.
Pflüger's tubes absent.	Pflüger's tubes absent.
Sex cells destroyed.	Sex cells absent.
Sex cords become tubules.	Sex cords as in female.
No Graafian follicles.	Anovular Graafian follicles.
Rete as in testis.	Rete as in ovary.

Whether the interpretation put forward is the correct one or not cannot be stated until further and fuller examination of similar cases has been made, but if it is granted that there is a chorionic anastomosis and that the ovary exerts its physiological activity before the testis, and that in the opossum there are secondary gonadic characters, there is no inherent flaw in the hypothesis.

(*c*) *The case of Bonellia.* The marine worm, *Bonellia viridis*, displays a remarkable degree of sex-dimorphism. The female has a plumpish green body about the size and shape of a plum, and lives under stones or in a hole in a rock, with a long, slender, terminally bifurcated, ciliated proboscis protruding for food-catching purposes. The male is a microscopic pigmy whose internal organs, save those concerned with reproduction, are entirely degenerate, and which lives as a

parasite within the body of the female. The fertilized eggs hatch out as free-swimming larvæ. If a larva settles down upon the sea bottom, it becomes, with few exceptions, and after a short period of sexual indifference, a female; but if by chance or perhaps through attraction it settles upon the proboscis of a female, it becomes a male. The sexual fate of a larva is determined by an accident of position. Baltzer (1914) took larvæ at various periods after they had settled upon a female, but before they had become completely male, and forced them to lead an independent life, and, as a result, he obtained intersexual

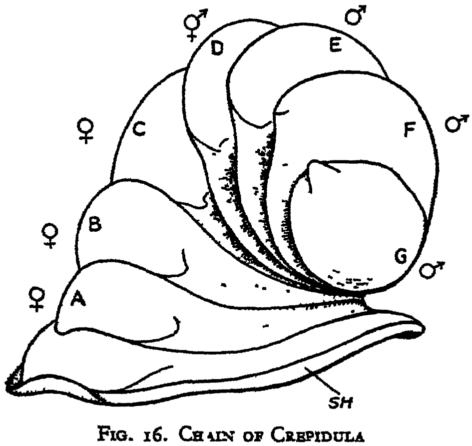

Fig. 16. Chain of Crepidula

forms, the degree of intersexuality varying with the length of time the larva had been allowed to remain upon the proboscis of the female. He stained the proboscis of the female with methylene blue and noticed that after the larvæ had settled down upon it for two or three days they also showed the blue stain. He concluded that the larvæ absorb material from the proboscis and that this is responsible for the arrest of growth and the direction of the sexual differentiation. The arrested pigmy male passes from the proboscis of the female into her mouth, and then, after a slight change, he emerges therefrom, and ensconces himself in the reproductive duct through which the eggs pass out into the water.

Baltzer has more recently (1925) shown that weak solutions of the green skin of the female proboscis are poisonous to many of the smaller forms of aquatic life and that the pigmy males of *Bonellia* are extremely sensitive to such solutions, over one in 3,000 being lethal; mere contact with the skin produces no ill effect, it is the absorption of substances that is fatal. The wall of the reproductive duct in which the adult males live has no poisonous action.

The efficacy of purely external stimuli to influence sex-differentiation is also seen in the case of the slipper limpet, *Crepidula*, which, introduced into this country from America, became such a plague to oyster fisheries. *Crepidula* lives gregariously in chains; the free-swimming young settle on older individuals and grow where they settle. Each individual after attaching itself passes through a phase of sexual indifference, next through a male phase, producing spermatozoa, then through a hermaphrodite phase, producing both spermatozoa and ova, and finally ends its days as a female, producing ova only. Gould (1917) found that in *Crepidula plana* the male phase occurs only if the individual settles in propinquity to a larger individual, larger and older, and, therefore, a female; but that if the individual is isolated and prevented from settling upon a female, it passes directly from the neutral to the female phase. A very similar state of affairs is recorded in the case of *Crepidula fornicata* by Orton (1909).

An ingenious hypothesis has been advanced to cover the observed facts concerning *Bonellia*, and in this matter the case of *Crepidula* is very similar. It is suggested that the sex-determining genes produce sex-differentiating substances unde

the direction of which the differentiation of the sex-organization is pursued. Goldschmidt (1923) supposes that in all the individuals there is at first an excess of male-differentiating substance, but that the production of the female-differentiating substance after a time overtakes this. Further, he supposes that the secretion of the proboscis of the female of *Bonellia* has the effect of accelerating the process of differentiation (as opposed to the process of growth), of antedating, as it were, states that in *Bonellia* sex is genetic. Larvae that are genetic females develop into females. Genetic males, developing without parasitism, pass through transitory intersexuality into females. Males that become parasitized develop into normal males if the process of sex-differentiation is completed during the male phase of development; if, however, the female phase sets in before the completion of the sex-differentiating process, such individuals develop as intersexes.

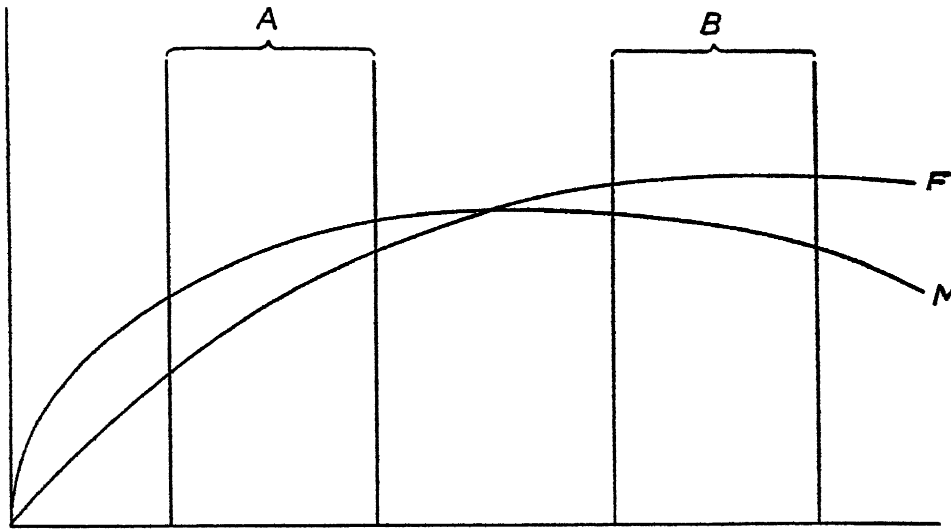

FIG. 17. *A* is the phase of sex-differentiation pursued at a time during development when the male-differentiating substances are effectively in excess; the result is a male type of sex-organization.

B is the same phase pursued under conditions when the female-differentiating substances are effectively in excess; the result is a female type of sex-organization.

the period during development when sexual differentiation occurs. When differentiation is rapid, the sex organization matures under the influence of the male-differentiating substance; when it is not accelerated, under that of the female-differentiating substance. The mode of sex-differentiation is determined by a varying physiological state in connection with varying environment and secretions from other individuals (fig. 17). Goldschmidt, in a more recent paper (1926),

The case of *Asterina gibbosa* (Cuénot, 1898) would appear also to belong to this group. At Roscoff every individual is first male and later female; at Banjuls the two phases overlap to a greater extent; at Naples the different types occur irregularly.

2. *Intersexuality through parasitism.* (*a*) *The case of Inachus and Sacculina.* Giard (1887) and later Smith (1906) described in detail the changes that occur in crabs parasitized by *Sacculina* and other parasitic

Crustacea. *Sacculina*, an internal parasite, is a cirriped crustacean, and part of its body projects to the exterior under the abdomen of the crab in which it is living, while root-like processes, which absorb the juices of its host, ramify to all parts of the crab's body, avoiding the vital organs and absorbing nourishment chiefly from the blood. It attacks males and females, and in both it causes atrophy of the sex-glands and consequent sterility. The only effect of this in the female is acceleration in the assumption of the adult sex characters. Parasitized males, however, gradually take on more and more of the female characters, their great claws become smaller and smaller, the abdomen broader, the swimmerets enlarge and become fringed with the hairs to which, in the females, the eggs are attached. Most of the affected crabs die, but in a few the parasite disappears and the reproductive organs are regenerated. In a female a normal ovary develops, in a but partially feminized male, a normal testis, but in a fully feminized male a sex-gland is regenerated, in which both ova and sperm are found: real male intersexuality is produced. Geoffrey Smith (1906), who investigated this problem, found that the blood of the normal female crab differs in chemical constitution from that of the male. It contains fatty substances which are absorbed by the ovaries and used in the production of the yolk of the egg. These fatty substances form an important part of the food of the parasite *Sacculina*. That which *Sacculina* absorbs cannot be used in yolk formation, and as the eggs cannot develop, the ovary degenerates. In the male these fatty substances are present in but small quantities. The parasite demands more and the whole physiology of the male crab is altered to meet this demand; the male thus assumes the female type of metabolism, and consequently the characters of the female.

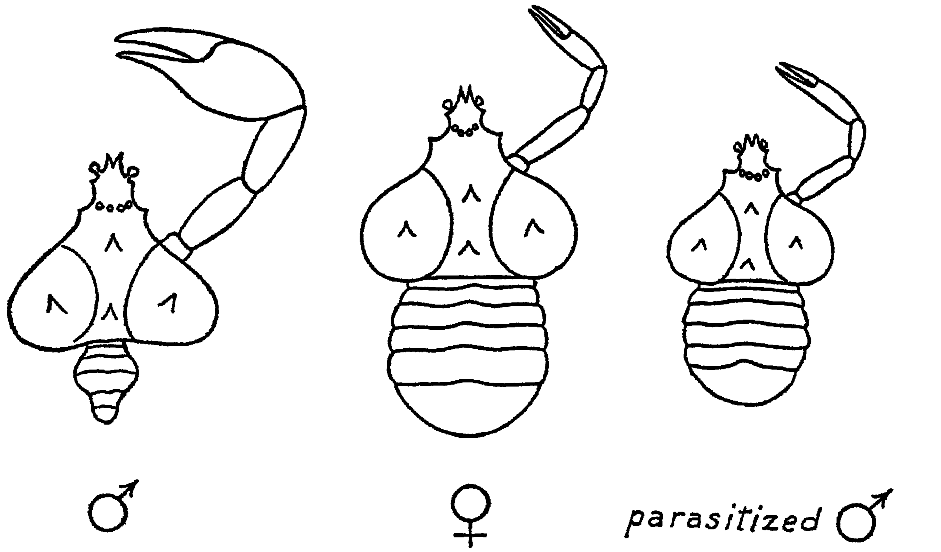

Fig. 18. The Case of *Inachus* and *Sacculina*

Robson (1911) states that the infection by *Sacculina* induces the maintenance of an abnormal quantity of fat in the liver and blood of the host. This condition resembles that found in normal females and males preparing for the molt, and in sexually mature females, the ultimate

destination of the fat being functionally similar in the case of mature females and the infected crabs. In all probability the ultimate fate of the infected crab is death from starvation, arising from its inability to obtain enough fatty material for itself and its parasite. A pink colored lipochrome is found in the blood of molting and infected animals of both sexes, while a rich yellow characterizes that of the sexually mature female.

The interest of this case is that it permitted Smith to question the validity of the conception that in all forms the gonads functioned as organs of internal secretion, contributing a peculiar product to the blood stream. Smith argued that the gonad, far from adding anything to the blood stream, removed something from it.

Goldschmidt, however, points out that it is not necessary to regard the change in metabolism as being the cause of the change in characterization, for it itself can be regarded as a secondary gonadic character. It is well established that the blood of the male is chemically different from that of the female (Steche, 1912; Geyer, 1913; Manoilov, 1922–1923; Gräfenberg, 1922), while Farkas (1903), Straus (1911), Lawrence and Riddle (1916), and Lipschutz (1916) have shown that the metabolism in the two sexes is markedly dissimilar, but so far it has not been possible to induce intersexuality by means of blood transfusion.

Potts (1906) has shown that the infection of the hermit crab, *Eupagurus meticulosus*, by the cirriped *Peltogaster curvatus* has the effect of diminishing immediately the size of the gonads and of suppressing their functions and that this is effected not only through direct action on the gonads but through interference with the general nutrition of the host. At an early stage of the external parasitism ova appear in the glandular part of the testis; no corresponding changes were traced in the ovary. The male type of characterization became transformed more or less towards the female type under the influence of the parasitism. The same sequence of events was observed also in the parasitized *Eupagurus prideauxi*.

It is to be noted that the development of ovarian tissue in the parasitized male crab is actually a process of regeneration. It is of interest to note, therefore, that in the case of the worm, *Ophryotrocha puerilis* (Braem, 1894), amputation of the genital segments of a female is followed by the development of testicular tissue in the regenerated portion. It is reasonable to assume that the conditions in which regeneration proceeds are responsible for the difference in the mode of differentiation.

(*b*) *The case of Thelia bimaculata.* Kornhauser (1916 and 1919) has shown that the male membracid, *Thelia bimaculata*, when affected by a species of the genus *Aphelopus*, one of the Dryinidæ, early in ontogeny, assumes the female coloration. The pronotum of the male is normally dark brown with a bright orange-yellow vitta on each side; the female is gray, the vitta being only slightly visible. The males of *Thelia* possess in diploid number twenty-one chromosomes, the largest of which is the X-chromosome. The female has twenty-two, two of which are large X's. Females are larger than males and testes develop earlier than ovaries. Parasitized females are not affected. The degree of the change-over in the male depends on the state of development of the parasites in the fifth instar of *Thelia* previous to the final molt. The parasite, a hymenopteron, lays its eggs in the nymph of *Thelia*. Fifty to sixty larvæ result and become full grown during the fifth instar of the host if the egg was

deposited in a *Thelia* of the first or second instar. The larvæ devour everything within the chitin of the host. If, however, they are only partially developed in the fifth instar, they do not kill and the host becomes an adult but modified.

Early parasitism results in retardation of differentiation of external genitalia in both sexes but no transformation. Parasitism of the male is followed by considerable increase in the body size, while in the case of the female it is followed by a slight decrease. Parasitized males assume female-type size of wing, size, pattern, and color of head, size of proboscis, size of legs, size of digestive tube, and size of abdomen. Parasitism of females results in a decrease in body size, but unaltered form, save that the ventral and terminal plates are soft and non-pigmented.

The results of parasitism are not due to the initial effect on the gonad, for in a parasitized male the testes may be normal. The changes are to be associated with change in nymphal metabolism. Male nymphs grow more rapidly, are smaller, darker, and are sexually mature when they become adult, the testes filling the greater part of the abdomen. The male is katabolic. Female nymphs develop slowly and become larger, store fat, and are anabolic.

Parasitism in the male brings about lower oxidation, storage of fat, retarded development, increased size. The external genitalia are laid down too early to be affected.

3. Intersexuality through gonadectomy. (*a*) *The case of the mammal.* Pearl and Surface (1915) have described the case of a cow with cystic degeneration of the ovaries which assumed the general appearance of a bull. Rörig (1900) and others have recorded instances of female deer with ovarian disease developing horns or antlers as in the male. The difficulty that exists in such cases as these is that of distinguishing between male and female characterizations on the one hand, and the agonadic form on the other. Tandler and Grosz (1913), for example, have shown that ovariotomy in the cow is followed by the assumption of a characterization which is intermediate between those of the normal male and female.

(*b*) *The case of the fowl.* The interrelationship between gonad and plumage characterization in the fowl can be demonstrated in the clearest possible way by an appeal to experimental gonadectomy and the implantation of gonadic tissues. The results of such experimentation by a considerable number of investigators (Pézard, 1924; Pézard, Sand, and Caridroit, 1924, 1926; Morgan, 1919; Roxas, 1926; Finlay, 1925; Goodale, 1916, 1918; *et alia*) are shown in table 6.

The fact that the presence of both ovarian and testicular tissues in the male is associated with hen-feathering is of interest in connection with the case of the gynandromorph fowl described by Macklin (this Journal, vol. 1, p. 329). It is established (Torrey and Horning, 1925; Cole and Reid, 1924; Crew, 1925; Zavadovsky, 1925; Brambell, 1926; *et alia* that the administration of thyroid extract to cocky-feathered cocks is followed by the assumption of feathers very similar to those characteristic of the hen of the same breed.

Cocky feathering in those cases in which there is sex-dimorphism in the color and structure of the plumage is commonly regarded as trustworthy indication that within the body there is, or was at the time when the plumage was developed, active functional testicular tissues; henny-feathering as an indication that there is, or was, active functional ovarian tissues. Gonadectomy in both sexes is followed, after a molt, by the assumption of a plum-

age which in its coloration is as that of the male of the variety to which the bird belongs, (save that in particolored breeders there is apt to be more white), while the barbules in the distal portions of the feathers of the hackle region are absent as in the normal male, but the plumage is much looser and far more luxuriant in its growth; the plumage characters of the capon and of the poularde are exactly alike. Since this is so, it is commonly argued that the goads exhibit an endocrine function, the ovarian internal secretion possessing the faculty of inhibiting the development of the plumage characters of the male. The fact that in certain breeds the cock is feathered as is the hen, is explained on the assumption that in their functioning, the testes of such a male are endocrinologically equivalent to the ovary of a hen. Such an interpretation is supported by the facts recorded in the above table, if it is assumed that in the case of a bird in which both ovarian and testicular tissues co-exist the internal secretion of the ovary is more potent or is produced in greater quantities than is that of the testes.

But there are several facts concerning the fowl, which, while emphatically

TABLE 6

SEX	OPERATION	EFFECT ON PLUMAGE	COMB AND WATTLES
♂	Castration	Becomes as that of a capon (male in color, looser, more luxuriant). If a hen-feathered cock, it becomes as that of a capon	Shrink
♂	Castration + implantation of testis	Remains as that of a cock. If testis from a cock-feathered cock is implanted into castrated hen-feathered cock, he still remains hen-feathered. If testis from a hen-feathered cock is implanted into a castrated cock-feathered cock, he will remain cock-feathered	Remain as those of a cock
♂	Castration + implantation of ovarian tissue	After molting, becomes as that of the hen of the breed and variety to which he belongs	Become as those of a hen
♂	Implantation of ovarian tissue	After molting, becomes as that of a hen, but more ruddy (warmer looking); tail sickles intermediate	Remain as those of a cock
♂	Implantation of extra testicular tissue	Becomes as that of the hen of the breed and variety to which he belongs; tail sickles intermediate	Remain as those of a cock
♀	Ovariotomy	Becomes as that of a capon of the breed and variety to which she belongs	Shrink
♀	Ovariotomy + implantation of ovary	Remains as that of the hen of the breed and variety to which she belongs, so long as implant remains as ovarian tissue	Remain as those of a hen
♀	Ovariotomy + implantation of testis	Becomes as that of a cock of the breed and variety to which she belongs	Become as those of a cock
♀	Implantation of testis	Remains henny, but more ruddy; tail sickles intermediate	Become as those of a cock
♀	Implantation of extra ovary	Remains henny; tail sickles intermediate	Remain as those of a hen

demonstrating the existence of secondary gonadic characters, do not support the contention that the gonads function as endocrine organs. On the contrary, they point to the conclusion that the relation of gonads and secondary gonadic characters is similar to that which obtains in the case of *Inachus*. In this discussion it is most important to note that the plumage characterization at the time of examination does not necessarily agree with the kind of gonadic tissue within the body at this time. Modification of the gonad does not affect feathers already grown. The plumage characterization is an accurate reflection of the condition of the gonadic tissue at the time when this plumage was developing.

The cocky-feathered laying hen. For example, there is no reason why a laying hen should not be cocky-feathered, or why a functional cock should not have the plumage of a capon.

The cocky-feathered laying hen is to be explained by the fact that at the time when this plumage was developing the ovary had undergone a more than usually complete involution. The bird then for the time being was without a gonad, and as, in the absence of the physiological activity of a gonad the plumage becomes as that of a capon, the plumage of the poularde began its development. Then the ovary resumed its activity, and the effect of its activity was to tighten up the plumage; it came into action, however, too late to model its structure. The present writer has in his possession a laying hen that has been henny, cocky, henny, and is cocky once more. (Lippincott has described a very similar case.) The head furnishings, the attitude, the behavior, have always been as those of a normal hen.

The developmental capon and poularde. The capon-feathered functional male is the result of a delayed action on the part of the testis during development. Such males are extremely common among White Leghorn flocks. Amongst White Leghorn cockerels there will be found three types: one that becomes sexually active at a very early age, with large erect combs and tight plumage and which continually attempts to crow and fight; another that develops as a bird that has been caponized within the first week of its life, its head furnishings remain bloodless, its body grows steadily in size to become long-legged and awkward, while its plumage is long and loose; and a larger class that falls between these two in respect of the attainment of sexual maturity. The breeder usually selects his males for breeding from among this latter class, and these in their turn produce the three types of male. The capon class matures very late and in many cases that have come under the observation of the writer, they have not attained full sexual maturity even in their third year. Examination will show testes equal in size only to those of the male chicken before the secondary gonadic characters have become expressed, and histologically revealing the fact that spermatogenesis is not complete.

Occasionally a developmental poularde is encountered and is in every way similar to the developmental capon save that she is smaller and that her face is distinctly more like that of the hen. She possesses an ovary of normal structure but one that has remained immature. The fact that the female is smaller than the male, even in such a physiologically agonadic specimen, would seem to suggest that perhaps size is largely determined by X-borne genes, these being duplex in the male, simplex in the female.

A case that cannot be interpreted if it is postulated that the ovary and the testis of the fowl elaborate an internal secretion

specifically different is that recently described by Greenwood and Crew (1926). A Brown Leghorn female chick was ovariotomized when four days old and into her body were implanted the chopped up testes of her brother. She became a typical masculinized female with large head furnishings and perfect cock plumage. At the age of seventeen months this bird molted and the new plumage was as that of a normal Brown Leghorn hen. At first it was thought that this was due to absorption of the testis implant and regeneration of the ovary, but, as the head furnishings still remained as those of the male, it was recognized that this could not be the case. Post mortem examination revealed a very small amount of highly degenerate ovarian tissue and a mass of testis tissue much greater than that usually found in a cock of the same size. The right gonad of the female, as is commonly the case in the ovariotomized hen (Domm, 1924; Benoit, 1924; Pézard and Caridroit, 1923 and Zavadovsky, 1922) had become differentiated as a testis in spite of the fact that the genotype of its constituent cells was XY.

At the time of the assumption of the adult plumage, this hen became completely cocky-feathered. If no gonadic tissue had been present during the critical period of the development of this plumage, this could have been cocky in color and structure, but loose and luxuriant as that of the capon. If at the beginning of this critical period, gonadic tissue had been absent or insufficient, the plumage would have started to develop the characterization of the plumage of the poularde, but, if shortly after this gonadic tissue of either kind, ovarian or testicular, had become sufficiently active, then though in its coloration and structure the plumage would have remained unaffected, it would have become tighter and closer to simulate that of the cock. It follows, then, that at the critical time of development of the first adult plumage ovarian tissue was either absent or insufficient, and that following this either ovarian or testicular tissues became physiologically sufficiently active or else that ovarian tissue was either absent or insufficient throughout, but that sufficient testicular tissue was present either at the beginning or else immediately after this. If the bird was a poularde, the plumage of which in the later stages of its development had been affected by the physiological action of ovarian tissue, then after a molt the plumage would have become completely henny, as indeed it did, the head furnishings would have always been as those of a hen of this breed and variety, which they were not, and only ovarian tissue would have been found post mortem, which was not the case. It is reasonable to assume that the second adult plumage was developed under the stimulus of a mass of testis greater than that usually found in a bird of this size. If this is the case, it is necessary to explain the association of abundant testicular tissues and henny feathering. It is to be noted that the testis tissue implanted was not that from such a male as a Sebright with henny feathering: it was from a Brown Leghorn, a breed in which the males are definitely cocky feathered. The facts of the case can be accommodated if it is assumed that ovarian and testicular tissues, in respect of their own individuation, exert demands upon the general economy of the same kind but different in degree, that the functioning of an ovary is physiologically more expensive than is that the testes, and that it is possible to supplement the demands of the testes so that they become equivalent to those of the ovary. This interpretation will explain the association of henny feathering and both ovarian and

testicular tissues as in Macklin's gynandromorph.

The assumption of male secondary gonadic characters of the senile hen. It is by no means uncommon for the senile female bird, wild and domesticated, to assume the plumage characters of the male of the breed and variety to which she belongs. Examination will reveal the fact that associated with this transformation there has been more or less complete destruction of ovarian tissue or a progressively diminishing physiological activity of this. Since, as has been shown, very similar results follow experimental gonadectomy, it is reasonable to interpret the phenomena as the result of pathological ovariotomy. Ordinarily during the succeeding years of the individual's life the oocytes in their growth make certain demands upon the general economy of the individual and maintain a metabolic level of femaleness, but, should the conditions be unfavorable for their growth as a result of the physiological exhaustion consequent upon excessive egg laying or from hæmorrhage or tumor growth, then, in the absence of the inhibitory influence of the growing oocytes, the plumage becomes as that of a capon which closely simulates that of a male of the breed and variety to which the individual belongs. In old hens it is quite common for the head furnishings to increase in size and to become as those of the cock. In such cases it is found that the plumage remains henny. Examination will reveal the presence of degenerate ovarian tissues in which tumor growth has occurred. It would seem that there is a definite relationship between the mitotic activity of the gonad and the size of the head furnishings.

The nature of the right gonad of the hen. Because it has been found that in the cases examined (Domm, 1924; Benoit, 1924; Zavadovsky, 1922) the right gonad of the ovariotomized hen develops into a testis, it has been argued that the hen is a constitutional hermaphrodite, that the right gonad which in the normal female chick ceases its development at or about the sixth to eighth day of incubation, is from its beginning a testis, but that being a testis in the presence of an actively developing ovary, it is not permitted to flourish. It is difficult to maintain such a thesis as this and in the light of more recent work it is far more satisfactory to explain the fact that this incompletely atrophied gonad becomes a testis in most cases following ovariotomy on the assumption that in spite of the fact that its tissues possess the XY type of constitution they are to a very considerable extent ambivalent in respect of their future differentiation and that their mode of differentiation is decided by the kind of physiological environment in which they find themselves. It will be remembered that in the case of the male, the products of the primary proliferation of the germinal epithelium cease their development at about the sixth day of incubation and are replaced by the products of a secondary proliferation which proceeds to become differentiated, in the case of the left gonad, as ovarian tissue. Any subsequent proliferation of germinal epithelium leads, if it leads anywhere, to the production of testicular tissue. Ovarian tissue is developed solely from a proliferation of germinal epithelium that more or less coincides with the sixth day of incubation. It follows that the difference between differentiation into ovarian or into testicular tissues is a reflection of a difference not inherent in the tissues themselves but in the environment in which this more or less ambivalent tissue develops. If and when the internal environment which obtains at the sixth day of incubation can be analyzed and recon-

structed, it will be possible to direct the differentiation of the products of any proliferation of germinal tissue into ovarian tissue. In this connection, it is of interest to note that Greenwood (1925) has found that, though in the majority of cases in which ovarian tissue has been implanted it ceases to develop as such but is replaced by the testicular, in certain cases it can continue its development as ovarian. It is not without significance that in quite a number of female hawks and owls there is a right ovary with normal follicles.

From this it will be foressen that if in a hen the ovarian tissue is destroyed, and if there is a recrudescence of activity in the rudimentary right gonad, or if a proliferation of germinal epithelium occurs, then testicular tissue will become differentiated, perfectly or imperfectly, and the phenotype, so far as plumage, head furnishings, spur, and behavior are concerned, will be transformed from that of the hen to or towards that of a cock. Greenwood (1925) found that no secondary proliferation of sex cords occurred in ovarian grafts in cases of ovarian implantation made later than the fourth day after hatching so that in the case of older fowls it may be expected that no new ovarian tissue will ever develop but that testicular tissue may develop in any female.

4. *Intersexuality due to the impress of external agencies (including temperature and salinity. (a) The case of the oyster.* In the diœcious species of oysters three intersexual individuals have been recorded. Kellogg (1890) described one in the American oyster, *Ostrea virginica*, and Amemiya (1925) two in the Portuguese oyster, *O. angulata*. These latter two contained eggs and sperm. The eggs were of ordinary size and shape, being similar to those of other diœcious oysters and much smaller than the eggs of species that are customarily hermaphroditic. Since Amemiya found these specimens among animals which had been kept in the tank for a considerable period, he inclines to the conclusion that the intersexual condition was definitely related to changes in nutrition. In this connection, the work of Orton (1921) on the native oyster, *O. edulis*, is of great importance.

In the case of forms such as those species of the oyster in which phenotypic maleness alternates with phenotypic femaleness, it can be concluded that the sex-chromosome mechanism which establishes the genotypic sex of the zygote is invariably overriden by environmental agencies. The deciding factor in the establishment of the sexual characterization of the individual is not the genotype; genotypic male and genotypic female alike are molded in their development by forces outside themselves. Spärck (1925), as the result of his extensive study of the native oyster (*O. edulis*), is led to the conclusion that it is the temperature of the medium in which the oyster lives that decides its sexual architecture through its direct effects upon the rate of general development, and not indirectly through its effects upon the numbers and general condition of the forms of life which constitute the food of the oyster.

It is not without significance that, as Weisensee (1916) has shown, certain species of *Anodonta* become hermaphroditic when living in isolated stagnant waters but are typically bisexual when in running water. It is probable that the instance of intersexuality recorded by Cuénot (1891) in the holothurian *Synapta inhaerens* and in the asteroid, *Asterinia gibbosa* (1898), and by Mortensen (1920) in certain ophiurids as well as the case of *Patella vulgata* to which reference is made below are all illustrations of the overriding of the

genotypic sex of both male and female zygotes by such agencies as temperature, salinity, or abundance or otherwise of nutriment.

(*b*) *The case of the limpet.* Gemmill (1896) described some cases of hermaphroditism in the limpet, *Patella vulgata*, in which the sexes are normally separate. The genital gland, ovary or testis, is single, and its products pass into one of the kidneys and reach the water by means of the kidney duct. No special genital ducts, no copulatory apparatus, and no secondary sexual structures appear to exist. In the limpet it is only when the individual has assumed its adult form that the generative gland begins to differentiate into ovary or testis. A number of specimens (3 in 250) were found in which the gonad was mixed, and its contents showed not only ripe—olive green—ova, but sperm—yellow—, segmented ova, and even ciliated freely moving embryos. Ovarian and testicular tissues in the gonad were not separated, but merged one into the other. The relative amount of ovarian and testicular tissue varied in different cases. The percentage of females (67) in a population of *Patella*, is independent of level, and consequently independent of time of feeding, since the high level are under water for a shorter period of time. Gemmill suggested that nutrition does not decide sex in this case because the ovary and testis are alike in bulk and there is no sexual ornamentation. These are insufficient reasons for such a conclusion. The work of Orton (1921) on this form is of great interest.

Nachtsheim (1923) records that in females of *Carausius* (Hymenoptera), the development of which proceeded at 25°C., the ventral portion of the thorax took on the red coloration characteristic of the male.

It would seem to be an established fact that there are three classes of animal: (1) those in which the genotype finally and irrevocably determines the sexual phenotype, the sexual characters being secondary genotypic characters; (2) those in which the sexual characters are a combination of secondary genotypic and secondary gonadic; and (3) those in which the action of the genotype is readily and usually overwhelmed by certain environmental agencies under the direction of which alone the sexual characterization is unfolded.

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THE PALÆOMORPHOLOGY OF THE HUMAN HEAD: TEN STRUCTURAL STAGES FROM FISH TO MAN PART I. THE SKULL IN NORMA LATERALIS[1]

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THE human head is always of special interest to anthropologists, who have measured and classified its varieties all over the world. But what is the human head, where did it come from and by what steps did it arise? The purpose of the present paper is to trace, so far as possible from available evidence, ten structural stages in the evolution of the vertebrate head from fish to man.

MORPHOLOGY OF THE SKULL IN FISH

In the Lower Devonian rocks of Great Britain, Russia and Canada, one finds the remote ancestors and relatives of the lobe-finned or crossopterygian fishes and of the dipnoans. The intensive studies of Pander, Traquair, D. M. S. Watson, Bryant and others in the structure of these fossil fishes have led to the now widely accepted conclusion that while neither the lobe-finned nor the dipnoan fishes are the direct ancestors of the land-living vertebrates, both are closely related to the still undiscovered tetrapod stem. On the whole, it is agreed, the lobe-finned fishes of the Devonian give us a fairly close picture of the morphology of the skull in the stage immediately preceding the emergence of swamp and land-living vertebrates.

The head, even of these primitive fishes, is already a highly developed structure. The skull consists essentially of internal or endocranial elements overlain by ganoine-covered surface bones, the latter being of the same nature as the scales on the body. The endocranium includes first, the bony capsules surrounding the nose, eyes and internal ears, and secondly, the bony trough that encloses the brain itself. As to the evolutionary history of the endocranium, considerable progress has been made in recent decades, but the present and following papers are concerned principally with the history of the dermocranium or surface skull.

In these primitive fishes (fig. 1, I) the dermocranium included the following series of elements: (1) roof bones on or near the mid-dorsal line, covering the nose, eyes, pineal organ and hind brain; (2) the maxillary series, including the premaxillæ and maxillæ of the upper jaw and the dentary or inferior maxillary of the lower jaw; (3) the circumorbital series of five plates around the eye; (4) the temporomandibular series; in the skull these plates, consisting chiefly of the squamosal and quadratojugal bones, cover the temporal region; they protect the upper jaw muscles and the back part of the primary upper jaw or pterygoquadrate. In the lower jaw this series includes the plates lying immediately behind and beneath the dentary, namely, the infradentaries or splenial, post-splenial, surangular; (5) the opercular series, covering the branchial chamber and the floor of the mouth.

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AMPHIBIANS

The oldest known stage of the tetrapods or higher vertebrates is that of the amphibians of the Lower Coal Measures of England Described very imperfectly by earlier authors, they have recently been restudied and redescribed by Professor D. M. S Watson of the University of London, in a memoir of the greatest importance to all students of the evolution of the vertebrates Watson, in common with other palaeontologists, regards these embolomerous amphibians as being practically the stem group of all higher vertebrates. In the arrangement of the surface bones of the skull these early gill-bearing forms (fig. 1, II) go far toward bridging the gap between fishes and amphibians. In fact they have inherited all the fundamentally piscine arrangement of the bones of the dermocranium described above, so that one may easily recognize most of the roofing bones, the maxillary series, the circumorbital series and the temporo-mandibular series Only the opercular series of the fish skull has disappeared, probably in connection with the change in habits There is nothing unusual about bones dwindling away and disappearing as we pass from older to later types The late Professor Williston of the University of Chicago brought forward much evidence showing that this reduction in number of elements, together with further differentiation of the remaining elements, is the normal course of skull evolution in vertebrates Hence the absence in the oldest amphibians of the whole series of opercular and gular plates is no bar to the derivation of the amphibians from fishes The place where the chief opercular bone formerly was is occupied in the earliest amphibians by a large notch, commonly called the otic notch The skin covering this region was already beginning to function as a tympanum or eardrum

REPTILES

The third stage is represented by a very primitive land-living form (*Seymouria*) from the Permo-Carboniferous beds of Texas (fig 1, III) This is technically classed as a reptile but retains many pronounced amphibian characteristics throughout the skeleton In this highly important form as studied by Cope, Broili, Williston, Watson and others, the otic notch is still large and the intertemporal and supratemporal bones are still retained The maxilla, as in fishes, does not extend upward on the side of the face, while the lacrymal is elongate and reaches from the orbit to the anterior nares.

The fourth stage is represented by one of the more primitive of the theromorph reptiles of the Permian of Texas (fig. 1, IV). Here the maxilla is beginning to grow upward, while the lacrymal has lost its extension to the nares. In the temporal region of the preceding stages the jaw muscles had been covered with an outer shell of bone, but in this form the

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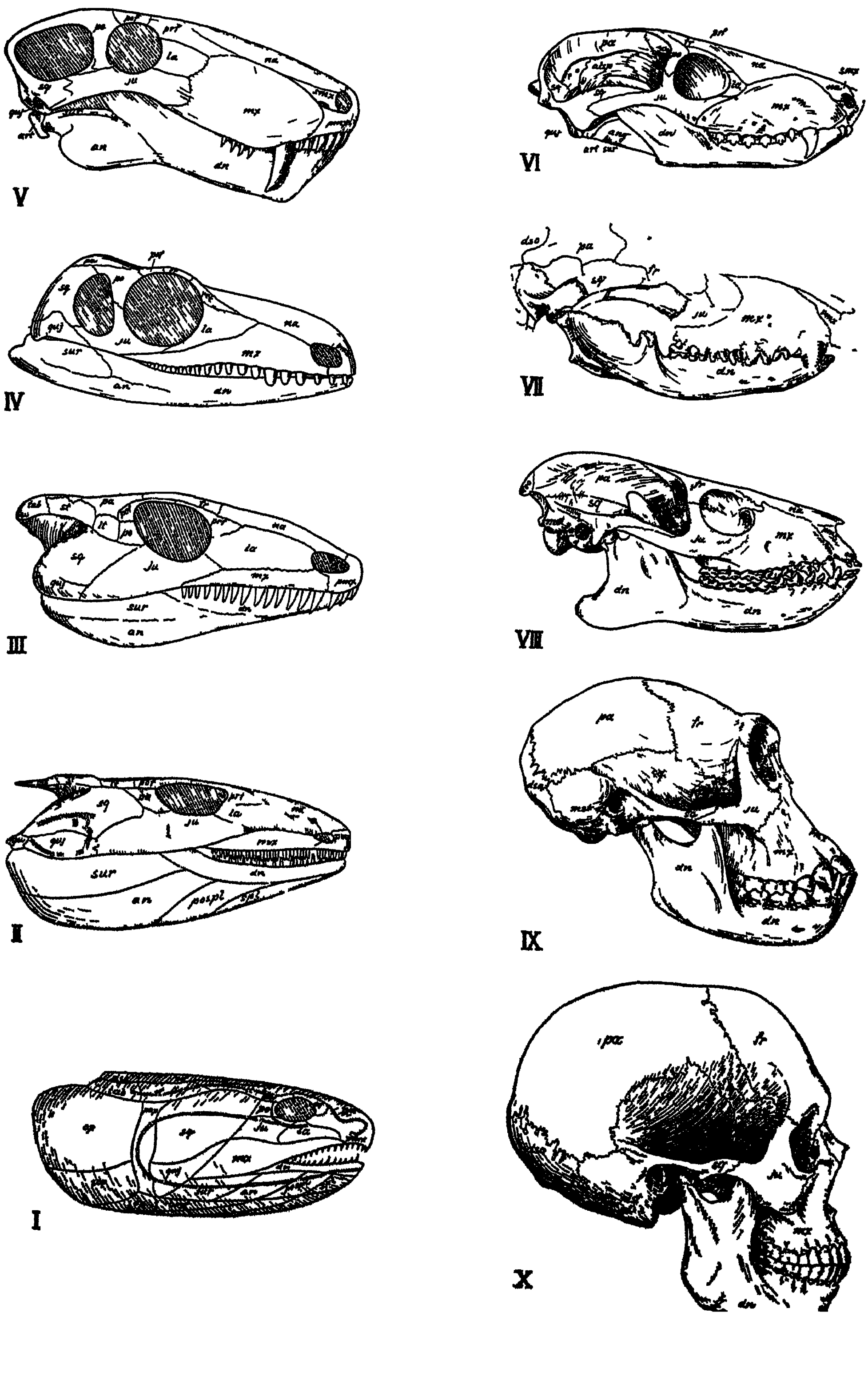
FIG 1 TEN STRUCTURAL STAGES FROM FISH TO MAN THE SKULL IN NORMA LATERALIS

I Rhipidistian fish, Devonian (essentially *Rhizodopsis*) After Traquair, Watson
II Embolomerous amphibian (*Eogyrinus*), Lower Carboniferous After Watson
III Primitive cotylosaurian reptile (*Seymouria*), Permo-Carboniferous After Broili, Williston, Watson.
IV Primitive theromorph reptile (*Mycterosaurus*), Permo-Carboniferous After Williston
V. Primitive gorgonopsian reptile (*Scymnognathus*), Permian After Broom
VI. Primitive cynodont reptile (*Ictidopsis*), Triassic
VII Primitive marsupial (*Eodelphis*), Upper Cretaceous After Matthew
VIII. Primitive primate (*Notharctus*), Eocene.
IX. Anthropoid (Chimpanzee)
X Man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shell had been perforated by a process of natural trephining in such a way that the middle of the area of origin had become thin and finally was perforated by the jaw muscle, while the outer margin of the area had become strengthened and built up into curved bars or arches. This opening and these bars are of profound morphological importance, since they mark the very beginning of the temporal fossa and zygomatic arch of man.

The fifth stage is furnished by one of the mammal-like reptiles from the Permian of South Africa (fig. 1, V), as described by Broom, Watson and other authors. Here the maxilla has already become the dominant element of the face. With the enlargement of the temporal fossa the surrounding bars of bone stand in clearer relief and we recognize easily the beginning of the mammalian zygomatic arch. In the lower jaw, the dentary sends upward and backward a strong process which overlaps the surangular. This process will be of critical importance in the further evolution of the skull.

The sixth stage is one of the smaller cynodonts from the Triassic of South Africa (fig. 1, VI). Technically these forms are classed as reptiles, but their whole skeleton shows a most interesting mixture of inherited reptilian and prophetic mammalian characters. In the skull the maxillary is the dominant facial element and the temporal fossa is almost wholly mammalian in type. The postfrontal bone has disappeared but the prefrontal, postorbital, jugal and lacrymal remain. In the lower jaw the dentary is now dominant and its ascending ramus is now reaching upward and backward toward the squamosal bone. The jaw elements behind the dentary, namely the surangular, angular and articular, together with the quadrate bone of the upper jaw, are much reduced in size in comparison with those of earlier members of the series. The dentition also is almost mammalian, being now thoroughly differentiated into incisors, canines, premolars and cuspidate molars.

MAMMALS

The most progressive cynodonts of the Triassic in many characters approach the more primitive carnivorous marsupials of the present time, especially in skull structure. But between them and the well known placental mammals of the beginning of the Eocene epoch lies a vast gap of at least several million years in duration. During the long ages in which the dinosaurs flourished the mammals remained small and inconspicuous and left as fossils tantalizingly few teeth and jaws, and hardly any skulls. A few years ago Mr. Barnum Brown of the American Museum of Natural History found embedded under the skull of one of the great dinosaurs of the Upper Cretaceous the fossil skull and jaw of a small mammal (fig. 1, VII) which has proved to be closely related to the existing opossum. Solely upon anatomical evidence it has long been recognized that the opossum is one of the most conservative types of mammalian living fossils now extant, and that in fact it has preserved most of the essential characters of a pre-placental Mesozoic mammal. Hence it is significant to observe that in the lateral aspect of the skull the Cretaceous and modern opossums retained a strong fundamental resemblance to the most progressive of the mammal-like reptiles.

In this seventh stage, however, the basal mammalian characteristics are well established. The most important fact is that the ascending ramus of the lower jaw has grown backward and upward until it has gained contact with the squamous portion of the temporal bone, where it

has formed a new joint, the temporomandibular articulation common to all mammals, but not yet achieved by any reptiles, with the doubtful exception of some of the diademodont division of the cynodonts. Meanwhile the lower jaw elements behind the dentary, namely the surangular, angular and articular, have disappeared, at least from the lateral aspect of the skull. To anyone who may doubt the validity of these inferences we may recommend the thorough study of the numerous papers of the late Professor E. Gaupp of Fribourg, one of the greatest morphologists of our time.

In passing from the reptilian to the primitive mammalian stage one sees clear examples of Williston's law of the progressive reduction of the skull elements. The supratemporal and intertemporal had long since disappeared. The cynodonts went further and dropped the postfrontal. The mammals went still further and cast off the prefrontal and the postorbital, leaving only the lacrymal and the jugal of the original five circumorbital bones.

But from the oldest mammals to man there will be no further reduction in the number of skull elements.

Light on the condition of the skull of the placental mammals during Cretaceous times has recently been gained from the highly important discovery by the Third Asiatic Expedition of the American Museum of six skulls and parts of skulls of Cretaceous mammals, which have recently been described by the author, in collaboration with Dr. G. G. Simpson of Yale University. These skulls lend much weight to the view of Huxley, Osborn, Weber and others that all the placental mammals of Eocene and later ages started from small insectivorous mammals. In spite of their far-reaching significance, I have not placed a figure of any of these skulls in the series showing ten structural stages for the reason that the exact arrangement of the sutural boundaries of the skull bones are for the most part not very clear. But in the form of the upper and lower premolars these Mongolian Cretaceous placentals afford an invaluable and long-sought-for stage in the evolution of the cheek teeth of the higher mammals, as I have shown in the December number of the American Journal of Physical Anthropology.

PRIMATES

Passing then to the eighth stage of the series, we come to the primitive Primates of the Eocene of North America, here represented by the genus *Notharctus* (fig. 1, VIII), excellent skulls of which are in my custody at the American Museum of Natural History. In the earlier mammals, as noted above, the postorbital bone had already disappeared, so that the temporal fossa was broadly continuous with the orbits. But the Primates, like certain other lines of mammals, notably the ruminant artiodactyls, soon found it advantageous to protect the eye by a postorbital bar and at the same time to brace the origin of the masseter muscle. Accordingly the frontal bone, which in the earlier vertebrates had been shut off from the orbits by the pre- and postfrontals, after the disappearance of these elements became the dominant element of the orbit and now sent downward a strong process, the postorbital process of the frontal, which met a similar process uprising from the jugal or malar bone. The eyes in the primitive stage are directed outward and forward. Meanwhile the angular process on the dentary or inferior maxillary had become prominent in correlation with the increasing obliquity of the pterygoid and masseter muscles. In the upper jaw the maxilla now effected contact with the frontal. The dental formula of *Notharctus*,

namely $I\frac{2}{2}$ $C\frac{1}{1}$ $Pm\frac{4}{4}$ $M\frac{3}{3}$ is undoubtedly more primitive than that of any higher primates.

The ninth stage of the present series is represented by the chimpanzee (fig. 1, IX), which is the least specialized in skull form of the existing great apes. From the detailed comparison of the jaws and teeth of the chimpanzee with those of the various species of fossil anthropoids referred to *Dryopithecus* and allied genera, I conclude that the skull form of female chimpanzees is not widely different from that of the inferred common ancestor of man and the higher anthropoids, and I find strong support for this view in many directions, especially in the masterly last work of that great anthropologist, Schwalbe.

Granting then for the moment at least, the view that in many respects the skull of a female chimpanzee is less advanced along the path of evolution than that of man, how does it differ from that of the vastly older and truly primitive skull of the Eocene primate *Notharctus?*

In the first place the chimpanzee has advanced beyond its Eocene predecessor in the forward shifting of the orbits, which are now directed completely forward so as to effect binocular, stereoscopic vision. Next, the postorbital septum now completely separates the orbit from the temporal fossa in the lateral view. With the assumption of brachiating habits the braincase has rotated forward and downward upon the column and the face has bent downward upon the basicranial axis. The premaxilla has fused with the superior maxilla and the greatest diameter of the latter is now approaching the vertical plane. Th maxilla sends forth two prongs on either side of the lacrymal, the former touching the frontal, the latter separating the lacrymal from the jugal. The dental formula has become reduced by the elimination of the first two premolars above and below, so that it is now the same as in man; the jaw is shortened and thickened, its angular process has also expanded and merges anteriorly with the mandible itself.

MAN

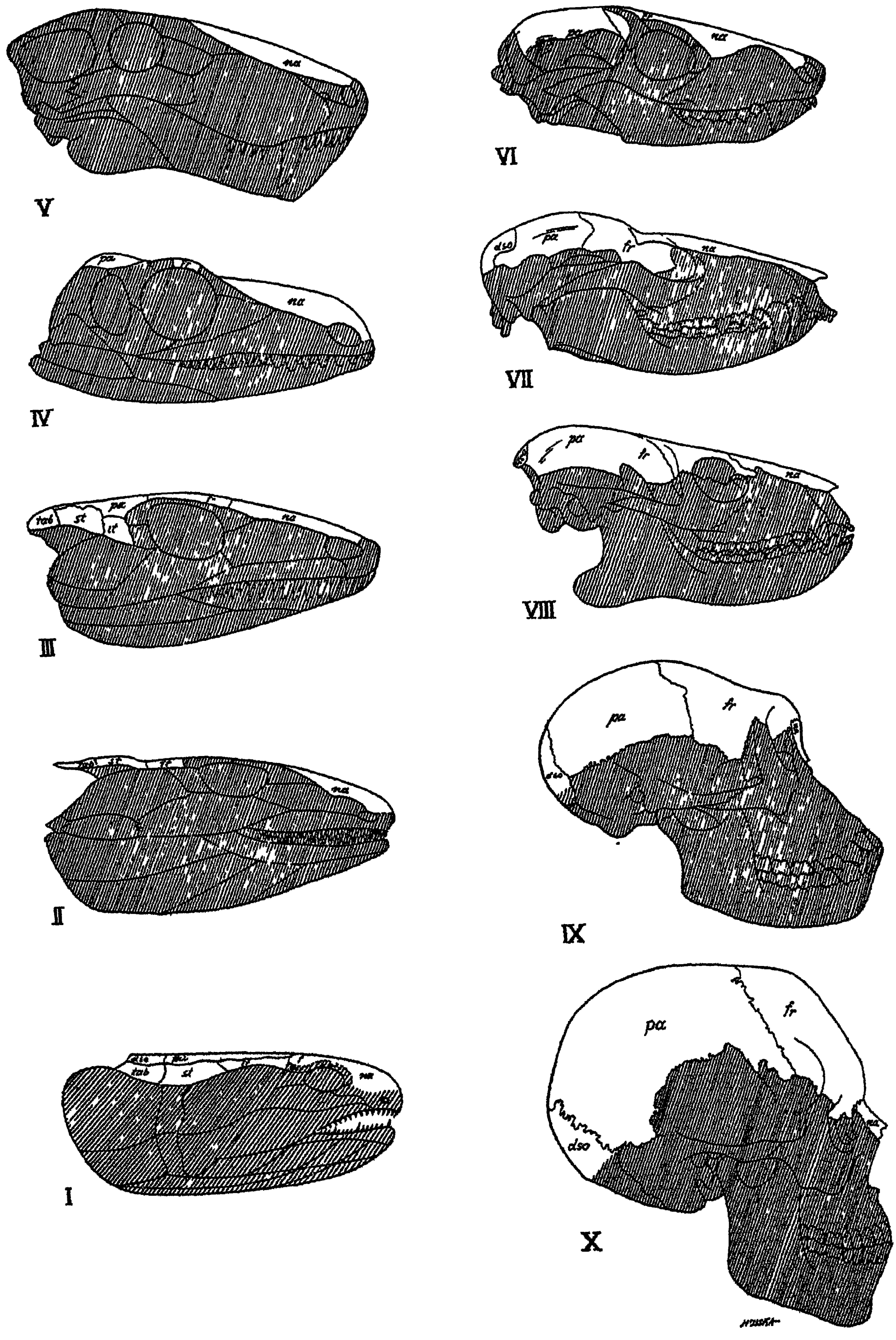
Viewed in this perspective the human skull (fig. 1, X) is seen to differ from that of the chimpanzee chiefly in the further development of the characters by which the chimpanzee differed from the earlier Primates. All the advances gained by the chimpanzee have in fact been carried much further in man. The greatest diameter of the face is now vertical rather than horizontal and the shortened jaws have been retracted beneath the forwardly-swelling and now enormous braincase. The dentition is enfeebled and a chin is present. But all these and many other differences are quantitative, not qualitative, and they measure the extent to which the human skull has outdistanced that of its humble relative, the chimpanzee.

CHANGES IN THE BONES OF THE SKULL

To recapitulate, the outstanding changes in the lateral view of the skull from fish to man appear to have been as follows:

Of the bones on the roof of the skull (fig. 2), namely the nasals, frontals, parietals, interparietals (or dermo-supraoccipitals) and tabulars, only the last disappear entirely in the mammals. As the brain enlarges these roofing bones are lifted into greater prominence, the frontals, parietals, interparietals and occipitals becoming the dominant elements in the great vault of the human skull.

The superior maxillary bone (fig. 3) begins as a slender, vertically shallow element, but by the time of the early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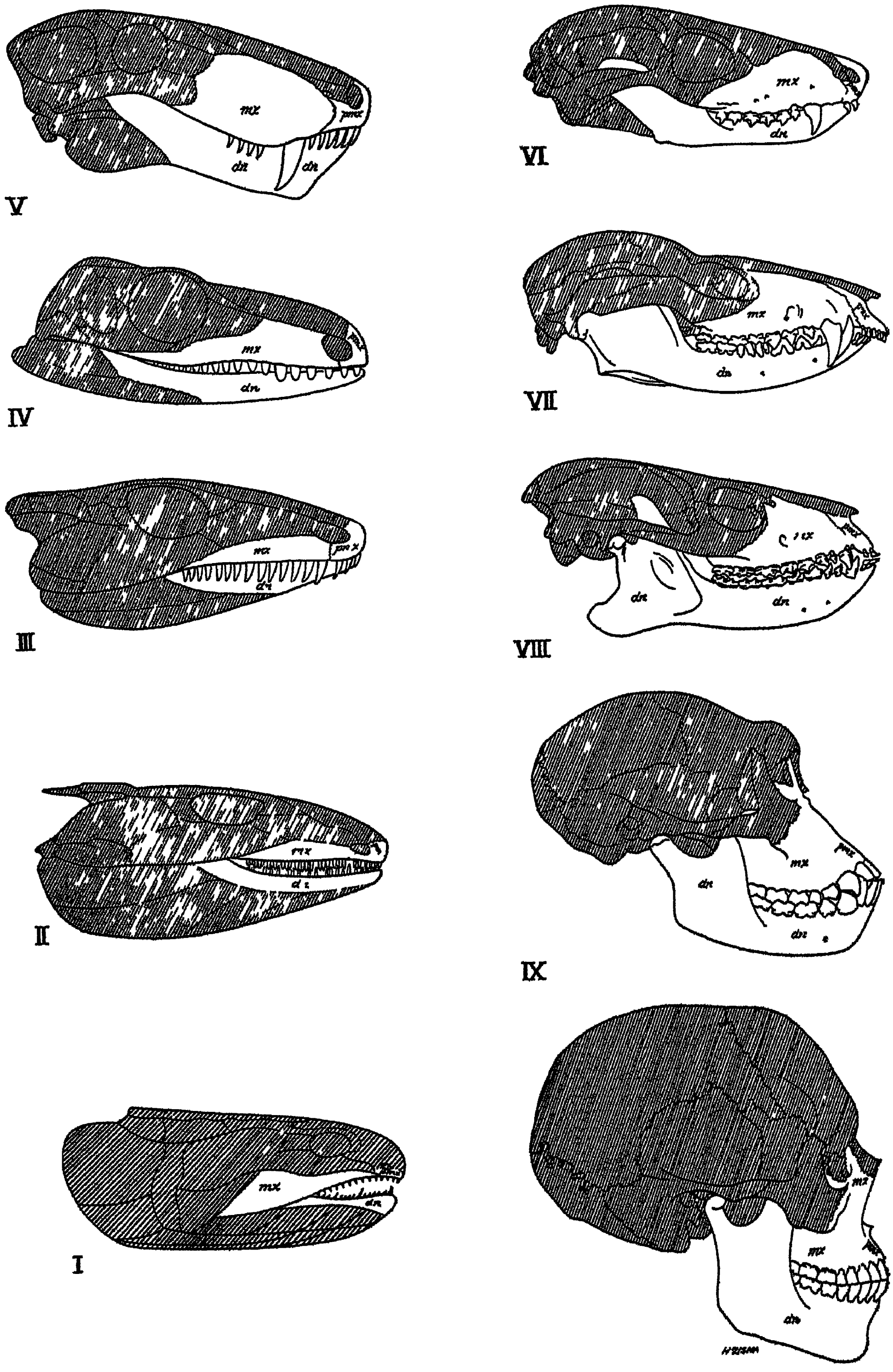
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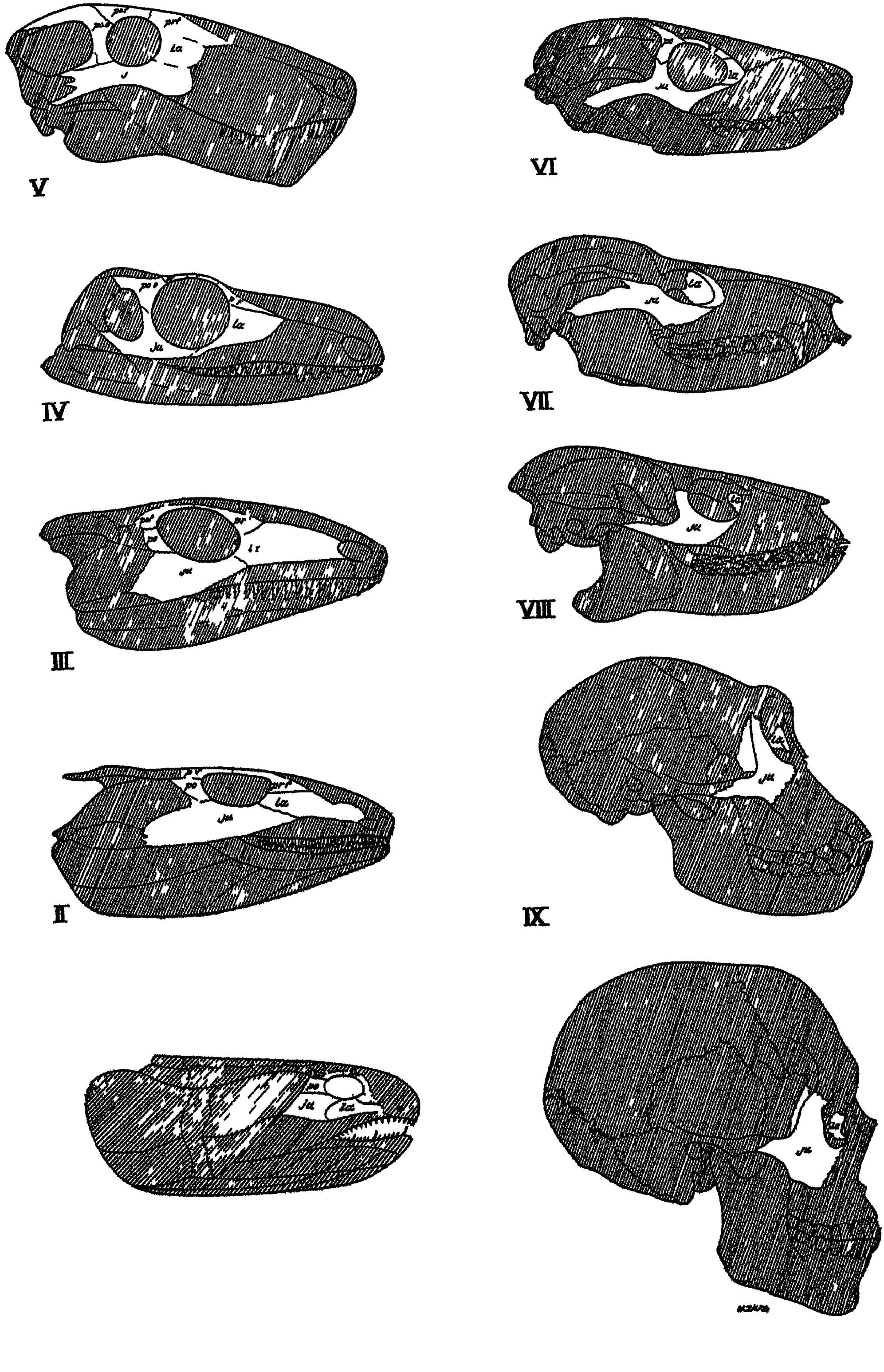
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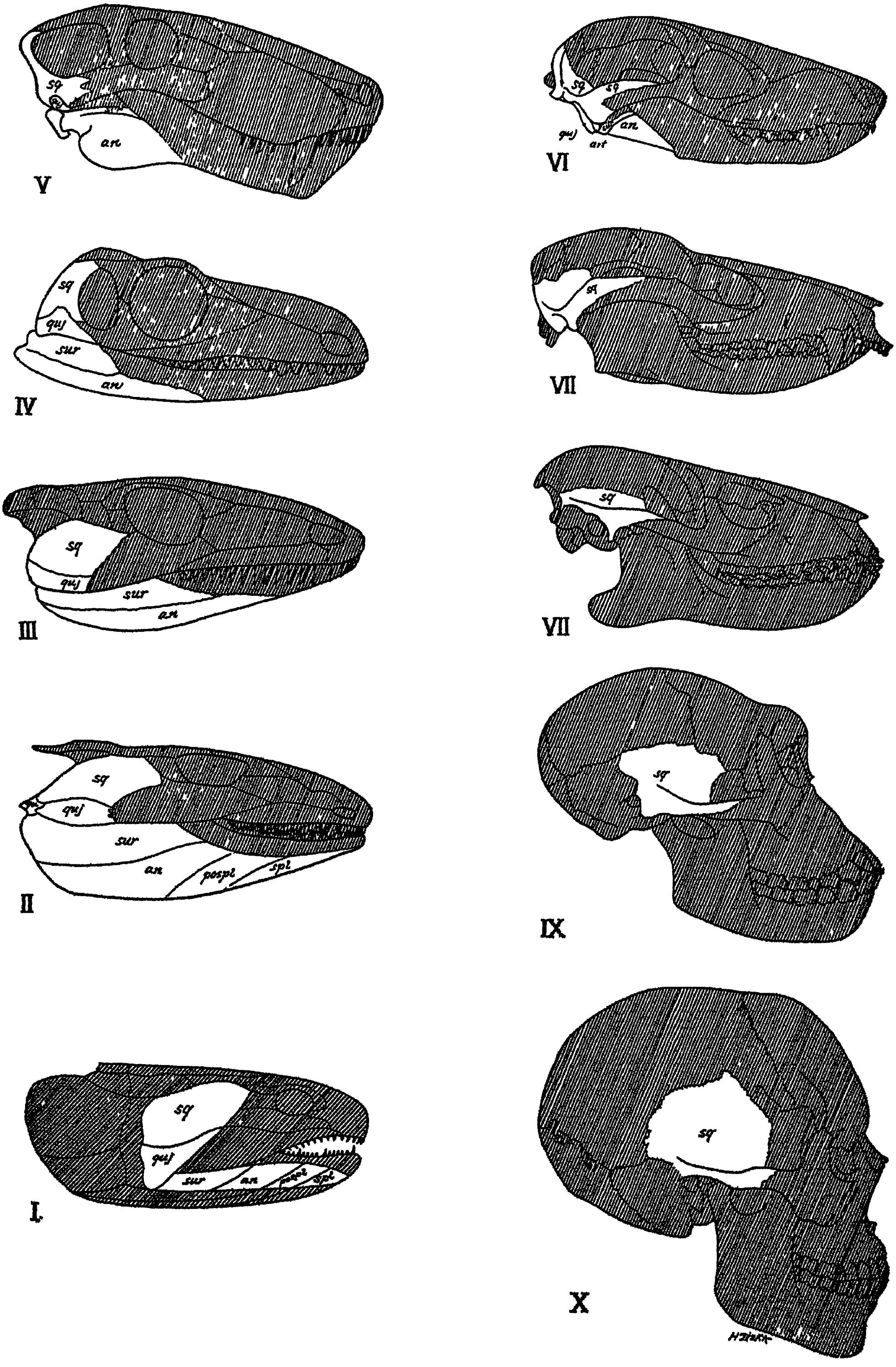
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mammal-like reptiles (fig. 3, V) it has extended dorsally and gained contact with the nasals. In the mammals (fig. 3, VII–X) its dominance is still more pronounced; one fork reaches the frontals while another fork finally separates the lacrymal from the jugal and the whole bone becomes shortened antero-horizontally and deepened vertically. In the anthropoids and man the premaxillæ early unite with the maxillæ.

The inferior maxillary (dentary) at first is confined to the anterior half of the mandible. In the higher mammal-like reptiles it becomes dominant, the post-dentary elements retreating before it. In the earliest mammals the ascending ramus of the dentary effects a new contact with the squamosal, the temporo-mandibular articulation, which is transmitted without further essential modification to man.

Of the bones around the eye (fig. 4), originally five in number, three (the prefrontal, postfrontal, postorbital) are eliminated by the time of the earliest mammals, so that man inherits only two of the original five, namely the lacrymal and the jugal or malar.

The temporo-mandibular series (fig. 5), originally including eight bones (the intertemporal, supratemporal, squamosal, quadrato-jugal, surangular, angular, postsplenial, splenial), suffers gradual reduction, until in the earliest mammals, as in man, only the squamosal remains, at least in the lateral view of the skull. In the mammals the squamosal has fused with the enlarged periotic mass and in the anthropoids and man the tympanic is added, the whole complex forming the temporal bone.

The changes in the endocranium and on the under side of the skull are no less plain and will be dealt with in other papers.

CORRELATION OF STRUCTURAL EVOLUTION AND CHANGES IN HABITS

At every successive stage of evolution advances in skull structure were dependent upon improvements in the brain itself, upon shiftings and enlargements of the parts containing the sense organs, upon modifications of the jaws and teeth, accompanying or accompanied by changes of habits. The skull in turn is closely integrated with both the active and the passive elements of the locomotor apparatus, a topic which will be developed elsewhere.

To each of the stages described above man owes certain "basic patents," or adaptive improvements which have been of critical importance in his survival. Thus to certain far-off Devonian air-breathing fishes man owes the general ground plan of the vertebrate skull, the combination of primary "gill-arch" jaws with sheathing or outer jaws, and each and every one of the twenty-eight normal skull bones which he still retains.

Next, he is indebted to the first amphibians for partially solving the innumerable problems caused by emergence from the water. These old pioneers cast off the whole series of bones that covered the branchial chamber and made for themselves an ear drum out of the skin around the notch where the opercular was formerly located. The early reptiles safeguarded most of the inheritance from their semi-aquatic ancestors, dropping only the inter- and supratemporals. To the first of the mammal-like series man owes the beginnings of his temporal fossa and zygomatic arch, and the dominance of the superior maxilla. From the higher mammal-like reptiles he has inherited the further development of the temporal fossa and especially the dominance of the

inferior maxillary or dentary bone of the lower jaw. To these progressive pro-mammals man can render thanks for the differentiation of his dentition into incisors, canines, premolars and molars, and apparently he can also thank them for the reduction of the numerous successional teeth to two sets, corresponding to the milk teeth and the permanent set.

The earliest mammals invented one of the most useful features of man's skull by eliminating from the masticatory apparatus all the elements lying behind the dentary and by establishing the temporo-mandibular joint. They also cast off the reptilian prefrontal, postfrontal and post-orbital bones and cleared the way for the final simplification of the bony scaffolding of the face.

To the earliest Primates, well schooled in arboreal life, man owes the first steps in the glorification of the eyes, which become increasingly dominant. These still lowly but thrifty forebears made good the loss of the reptilian postorbital bar by elaborating a new one from conjoining processes from the frontal and jugal (or malar) bones.

But still greater was our debt to the arboreal pro-anthropoids, those intelligent beings who elected to develop sight at the expense of smell. These skilled acrobats, moving in a vertical position, met and solved a new series of problems connected with the turning downward of the skull upon the upright column. They also made the first notable attempts to shorten and deepen the face and even took a long step toward enlarging the brain and brain chamber.

Starting with these and many like advantages gained during a long training in arboreal life, it was the task of our relatively nearer precursors (beginning possibly in Miocene times, or earlier) to re-adapt all these arboreal adaptations for a life on the ground and to take the final steps upward that have brought humanity to its present relatively high level of intelligence.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will usually appear in each number one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that The Quarterly Review of Biology *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* The Quarterly Review of Biology, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

A PHYSIOLOGICAL THEORY OF HEREDITY

Being a review of *Physiologische Theorie der Vererbung*, by Richard Goldschmidt. Berlin (Julius Springer), 1927. 4½ x 7; vi + 247, 59 figs. Reichsmark 15.

By W. E. Castle, Harvard University

An attempt has been made in this book to extend to heredity in general an explanation previously formulated by the author for the peculiar phenomena of sex determination and sex expression in the gipsy moth. Goldschmidt's fruitful discoveries in this field are well known to biologists, and any generalizations which he may have deduced from them merit careful consideration.

The bisexual state common in all the higher animals, in order to function properly for the perpetuation of the species must be represented in two—and only two—very different kind of individuals, males and females. Each of these must produce a different kind of reproductive cell or gamete, the female producing eggs, the male sperm. The female usually possesses also apparatus for the reception and, if necessary, for the storage of sperm, as well as for egg-laying, or the bringing forth of living young. The male must have suitable organs for bringing the sperm which he produces into effective relation with the eggs, either within or without the body of the female.

Apart from these essential or primary sex differences, there are other secondary ones which permit of the ready recognition of the sexes, such as the beard and voice of man, and the plumage of birds. The entire complex of one sex or the other is normally inherited as a whole. If this does not happen, disastrous consequences follow, as in the crossing of different geographic races of the gipsy moth, *Lymantria*, studied by Goldschmidt. Here individuals are produced which show mixed or intermediate sexual states affecting in varying degrees both primary and secondary sex organs. Such individuals, called intersexes by Goldschmidt, are usually incapable of reproduction because they possess neither one nor the other of the two interlocking sets of sex mechanism necessary for normal reproduction.

There is a certain analogy between the inheritance of the alternative sex states, male and female, and the inheritance of alternative dominants and recessives in Mendelian inheritance. This was recog-

nized by Mendel himself, as shown by his posthumously published letters, and it has been the basis of fruitful subsequent study of sex inheritance.

But there is this difference between the two cases, that a race may contain, and usually does contain, only *one* of two or more Mendelian allelomorphs, whereas maleness and femaleness must both occur in the same interbreeding population, if sexual reproduction is to occur.

It is not certain, therefore, that everything which happens in sexual reproduction will find its counterpart in heredity in general.

Goldschmidt assumes, at the outset, that all inheritance is Mendelian, and that its operation is through genes contained exclusively in the chromosomes. In other words he accepts in full the basic conclusions of the Morgan school as to the mechanism of heredity, although he finds much to criticise in matters of detail. He seeks to go beyond the findings of the Morgan school and explain *how* the genes operate in producing their end results.

Goldschmidt takes the operation of the sex genes (in sex determination) as his point of departure. A quantitative relation of such genes normally determines whether maleness or femaleness shall be expressed in the zygote. Thus in the squash bug, in *Drosophila*, and in a great many other animals including man, one X determines maleness but 2X femaleness in all their varied forms of expression. There is no other point of organic equilibrium for the zygote except maleness or femaleness. These are expressed in their entirety, one or the other, according as a single or a double dose is present of the genes contained in the X-chromosome. The facts so far are incontestable. Goldschmidt goes further and assumes that there are specific genes for maleness (M) and femaleness (F). Here he is on less certain ground. He bases the assumption on the wide variety of characters in whose production genes are known to be involved. Sex is just one more case. But Riddle has shown in the case of pigeons and Lillie in cattle, that an embryo which would otherwise be a female may be changed into a male, or *vice versa*, without disturbing the gene apparatus, but merely by manipulation of other conditions, as for example the oxidation rate of the egg cytoplasm, or the chemical composition of the blood of the embryo. These findings are supported by a large amount of experimental evidence on other animals. Further Bridges has shown that *all* the chromosomes of *Drosophila* have a "net influence" on the determination of sex, directing the development of the embryo either toward maleness or toward femaleness. Now it is possible to assume that in these chromosomes there are specific genes for maleness and femaleness, but it is not possible to make this assumption for an influence wholly outside the chromosomes, such as an environmental condition. The assumption is therefore superfluous that specific genes for maleness and femaleness are involved in sex determination. It may be only that the embryo in development may according to circumstances assume one or the other of two alternative forms. The determining factors are partly internal, partly external. No one refers to the external factors as genes for maleness or femaleness; why need we assume that the internal ones are such?

It may be suggested that this line of argument is destructive of the entire theory of the gene, because many characters for which we postulate genes are influenced in their expression by external conditions also. By gene we mean a substance or molecule or material influence of some sort occupying a particular locus

in or on a chromosome and capable of influencing the development of some character in the organism. We hesitate to extend the theory of the gene to the organism-as-a-whole, lest it cease to have utility. Who has assumed the existence of genes for vertebrateness and genes for arthropodness? Perhaps if we could cross the two groups, some one would have the hardihood to postulate a multiple factor system for each. The current explanation of blending inheritance is scarcely less fanciful. But until such cases as phylum differences have been analyzed into genes, we may properly object to the assumption of specific genes for maleness and femaleness. Nevertheless we must allow Goldschmidt to make the assumption in order to formulate his theory, but like the attorney for the defense we register an objection with the court.

Goldschmidt's formulation proceeds as follows:

1. Each sex contains the genes for the differentiation of both sexes.

2. Of these genes one sort is in the X-chromosome (F in *Drosophila*, M in *Lymantria*), so that in one sex it is present in a double dose, in the other in single dose.

3. The other sort of sex gene (M in *Drosophila*, F in *Lymantria*) is present in the autosomes of *Drosophila*, and in the Y-chromosome of *Lymantria*. In *Lymantria* modifying factors of sex are assumed to be present in the autosomes also.

4. The relative quantity of the sex genes determines the sex of the embryo, the operation of each sort of gene being proportional to its quantity.

5. Normally the dosage of genes must be such that the quantity of the sort lying outside the X-chromosomes shall be greater than that of the sort lying in *one* X-chromosome but less than that lying in *two* X-chromosomes.

6. Proportional to the quantity of each kind of sex gene is assumed to be the rapidity of the corresponding sex determining reaction.

7. Male and female sex determining reactions occur simultaneously but the one which progresses more rapidly controls differentiation.

8. The reactions consist in the production of substances controlling sexual differentiation, which progresses normally only in one of two possible (male or female) directions.

Goldschmidt regards points 1, 2, 3, and 5 as of especial importance in relation to the question of sex determination, the others as the basis for his general theory of heredity. Point 1 he regards as beyond doubt. If one concedes the assumption that there are specific genes for maleness and femaleness, then it must be granted further in view of the experimental evidence that every individual contains genes of both sorts, that is has at the outset the capacity to develop either into a male or into a female. It is inconceivable to him that there should be wholly sexless individuals. But such individuals should be conceivable if maleness and femaleness are produced by specific genes. Mutation in or loss of these genes should be capable of producing either individuals which lack the genes for one sex, or those which have no sex genes whatever. The fact that such individuals are unknown argues against the fundamental assumption that specific sex genes exist.

Points 4 and 5 are deduced by Goldschmidt from the important results of his crosses between different geographic races of the gipsy moth, *Lymantria*. By certain of these crosses he has shown that individuals are regularly produced which in their sexual characters are intermediate between males and females, and which he calls "intersexes."

The normal result of intra-racial matings is the production of equal numbers of males and females. When intersexes are produced, they occur as a modification of one or the other of the normal sex groups, but not both. Accordingly Goldschmidt designates them *female intersexes* when they occur in association with normal males and *male intersexes* when they occur in association with normal females.

Races may be grouped, as regards their genetic properties, into the strong, the neutral, and the weak. A female of a weak race crossed with a male of a strong race produces female intersexes, whereas the result of the reciprocal cross is normal in F_1, but includes male intersexes in F_2. Neutral races give a normal result when crossed with any other race. A normal result is also produced by crossing weak with weak or strong with strong. It is only crosses of weak with strong that produce intersexes. There are different degrees of intersexuality forming a complete transition from male to female, or *vice versa*, and ending with the complete transformation of what is expected to be one sex into the other. Different strong or weak races produce different degrees of intersexuality in crosses. Thus a female of weak race *A*, with a male of strong race *M*, produces along with normal F_1 males, females only slightly intersexual (that is showing male-like characters). But a female of the same weak race *A* mated to a male of strong race *N*, produces females moderately intersexual (male-like), and if mated with a male of strong race *O* produces only strongly intersexual females (in addition to the usual 50 per cent of normal males). Thus among strong and weak races there are different degrees of strength and weakness.

This series of facts is regarded by Goldschmidt as showing not only that there are separate specific genes for maleness and femaleness but that these vary quantitatively from race to race and on the basis of these quantitative variations accurate predictions can be made as to the results of particular matings.

Similar conclusions are drawn from a review of Bridges' experiments with triploid and partially triploid individuals of *Drosophila*. Bridges showed that triploidy or tetraploidy affecting all chromosomes alike does not alter the sex, but if the autosomes become triploid while X remains diploid an intersex results (a female showing male characters). On the other hand if X becomes triploid while the autosomes are diploid, a "superfemale" results. That is X has a female producing tendency, and the autosomes a male producing tendency. What the zygote becomes, depends on the proportions in which the different kinds of chromosomes are present. The later results of Bridges indicate that chromosome IV as well as X has a net female producing tendency, leaving the net male producing tendency to chromosomes II and III only.

It is undeniable, in view of the very positive results of both Goldschmidt and Bridges, that chromosomes as wholes do have a very positive influence in sex determination. The X in *Drosophila* has a female determining influence, that of *Lymantria* according to Goldschmidt is male determining. With racial variation, which undoubtedly involves changes in chromosome constitution, the sex-determining influence of chromosomes varies. Whether there are particular parts of chromosomes or special genes which exert an influence toward male or female differentiation remains to be demonstrated.

Goldschmidt explains the varying degrees of intersexuality observed in his cultures in the following way. He observes that in individuals only slightly

intersexual the organs affected are only those latest to be differentiated. As the degree of intersexuality increases, additional organs are affected which were earlier differentiated, until in extreme cases even the earliest differentiated organs become affected and a complete sex transformation results. He concludes that an intersex is an individual which up to a certain point develops as of one sex (as determined by the ordinary X-Y chromosome apparatus) but beyond that point develops as an individual of the *opposite* sex. As to the *fact* of an abrupt change in sex character during the process of development he is very positive. The workers on *Drosophila*, so far as I know, have not observed this, but Crew thinks something of the kind occurs in amphibian and mammalian intersexes. Why does a change in sex differentiation occur during the development of intersexes? Goldschmidt's explanation is as follows: 1. The quantitative relation of the male and female sex genes determines which at the outset shall be operative. The greater controls. Thus a genetic male produces more *male stuff* than female stuff, and a genetic female produces more *female stuff* than male stuff. The kind of stuff which is in excess controls differentiation. Ordinarily the initial excess persists throughout development but in an intersex it is replaced at some point by an excess of the opposite sort of stuff which then takes control. 2. The sex gene which is greater at the outset produces sex stuff more rapidly and so holds control so long as it has suitable material to act upon. But it may use up this material sooner because of the very energy of its initial enzymatic activity and so its product may later fall off, whereas the originally weaker gene acting with more moderation may later have a greater total output and so take control.

This basic conception, if I have rightly understood it, is elaborated by Goldschmidt at great length and with endless diagrams which serve rather to confuse than to clarify the situation in the mind of the ordinary reader. Such a reader would like to see the alleged fact substantiated that in the development of an intersex there is a definite change during ontogeny from femaleness to maleness or *vice versa*, and not a balanced relation of maleness and femaleness *throughout development*, as has been commonly supposed. Goldschmidt does not think it necessary in this publication to submit evidence in support of his statement that such a change in sex occurs. He refers the reader to earlier and more detailed publications.

The greater part of his book is devoted to the extension to heredity in general of the explanation formulated for sex inheritance. The phenomena of Mendelian inheritance including dominance are regarded as consequences of 1) differences in quantitative value of genes, 2) in consequent rates of reaction, and 3) production of formative stuffs, limited by 4) the catalytic nature of genes in general.

A gene is considered to be a material particle of a particular quality present at the beginning of development in definite quantity in a particular chromosome. It begins its action to produce a formative stuff as soon as development begins, but this will not become effective until it has the proper quantitative relation to other competing formative stuffs. Thus a recessive gene has no visible effect so long as the corresponding dominant is present along with it. The genes on Goldschmidt's view are catalytic substances—sometimes he suggests that they are autocatalytic—, the formative stuffs which they produce are hormone-like in action.

It is difficult for the ordinary student of

genetics to estimate the value of this theory which involves many unproved assumptions as to the chemical events occurring in ontogeny. To the ordinary geneticist a gene in the guise of an autocatalytic enzyme is as incomprehensible and much less usable than when designated simply *A* or *a*. Only an expert biochemist working at the elbow of a geneticist will be able to say whether Goldschmidt's theory is a step forward in the explanation of heredity, or pure bunkum. But Goldschmidt's genetic studies of *Lymantria* have brought to light many important and significant facts. Possibly a simpler explanation than his may be found for some of them, but at any rate they merit careful attention and verification, if possible, on other organisms.

BRIEF NOTICES

EVOLUTION

HOLISM AND EVOLUTION.

By J. C. Smuts. *The Macmillan Co.*
$3.50 $8\frac{1}{2}$ x $5\frac{1}{2}$; vii + 362 *New York*

This is a remarkable book. There are few persons in the history of the world who, having pursued throughout their adult life an active political career and achieved in it such success as is implied by a premiership, are either inclined or able then to make a first-rate contribution to the philosophy of science. And precisely this is what General Smuts has done. *Holism and Evolution* will stand comparison on its merits with anything that has yet been written on emergent evolution.

The viewpoint and scope of the book are indicated by the following quotation:

> This work deals with some of the problems which fall within the debatable borderland between Science and Philosophy. It is a book neither of Science nor of Philosophy, but of some points of contact between the two. To my mind it is the surface of contact between the two that will prove fruitful and creative for future progress in both, and to which special attention should be directed. Some border problems between the two are here considered in the light of recent advances in physical and biological science. And a re-examination of fundamental concepts in the light of these advances reveals the existence of a hitherto neglected factor or principle of a very important character. This factor, called Holism in the sequel, underlies the synthetic tendency in the universe, and is the principle which makes for the origin and progress of wholes in the universe. An attempt is made to show that this whole-making or holistic tendency is fundamental in nature, that it has a well-marked ascertainable character, and that Evolution is nothing but the gradual development and stratification of progressive series of wholes, stretching from the inorganic beginnings to the highest levels of spiritual creation. This work deals with our primary concepts of matter, life, mind, and personality in the light of this principle, and discusses some of the problems of Evolution from this new point of view.

The remarkable things about the book are first its originality and freshness of viewpoint, and second the extraordinary familiarity which the author displays with the trends of inquiry and results in various fields of science. To be sure a good deal of General Smuts' reading of science has obviously been from second rather than first hand sources. But on the whole he has kept his balance very successfully. We urge all biologists to read the book, whether they agree with its viewpoint and conclusions, or do not.

EVOLUTION NOT IRRELIGIOUS. *Some General Aspects of Evolution and Relations to Religion.*

By Walter C. Kraatz. *Walter C. Kraatz*
20 cents 5 x 7; 28 (paper) *Akron, Ohio*

A "reconciliation" document by the

assistant professor of biology in the University of Akron, Ohio. That man was descended from a monkey is branded as a "common misconception." But just what he was descended from is not made clear. However, "man's evolution is demonstrated."

A static mind must have a static idea to cherish and fight for. The others being taken from under them so completely by the more mathematically demonstrable sciences, they concentrate their attacks upon organic evolution, or especially that part, evolution of man, where they know that their emotional appeals may strike a popular chord. Man is unavoidably somewhat egotistic and proud of his high degree. Like the 'new rich' in human society he often disdains his poor beginnings. This policy is not commendable, not Christian-like. It is prejudiced and entirely unscientific. The scientific attitude must be secured if the consideration of man is going to be made as fairly and as judiciously as the consideration of the rest of the world. The scientific attitude and method are the same in all the sciences: But since biology is not a mathematical science like astronomy we must presumably for a few more centuries bear with the semi-occasional attacks of the opposition.

Magna est veritas!

MAN CREATED DURING DESCENT *at the beginning of the New Stone Age, that is, not more than about five or seven dozen centuries ago.*

By Rev. Morris Morris.

Marshall Brothers, Ltd.

3s. 6d. $7\frac{1}{2} \times 5$; 111 *London*

Here comes a new fundamentalist, much higher-toned than Mr. Bryan and his like. Mr. Morris was once a research scholar in geology in the University of Melbourne. He has all the technique of scholarship and documents his case from separately unimpeachable scientific sources, but some of the authors quoted will be surprised to see the conclusions to which their innocent and carefully safeguarded statements lead, when skilfully marshalled by Mr. Morris to support his thesis. The general idea of this thesis is that when business is dull, or as the occasion seems to require it, some special creating is done. In the intervals evolution by natural causes goes on. The last time any considerable job was done in the creating way was at the end of the Old Stone Age. Man was then made, more or less just like that! The proof is found in the relics of the neolithic culture. They were made by *men*. Mr. Morris says so. The paleolithic artefacts were the products of "individuals of a lower species," erroneously called "man" by archeologists and anthropologists. The book is an interesting example of how a shrewd dialectician can use sound data to establish a ridiculous conclusion.

SCIENCE AND ULTIMATE TRUTH.

Fison Memorial Lecture, 1926. Delivered at Guy's Hospital Medical School, March 25, 1926.

Rev. W. R. Inge. Longmans, Green and Co.

65 cents $5\frac{1}{2} \times 8\frac{1}{2}$; 32 *New York*

Anything that the distinguished Dean of St. Paul's writes is sure to be interesting, stimulating, and clear-headed to a degree not commonly attained in the lucubrations of the reverend clergy. This lecture is a contribution to the literature of reconciliation. But it has a higher and different tone than the efforts in the same direction of some of our distinguished scientific colleagues in this country, as the following passage sufficiently shows: "I know that religion, science, and art are all jealous of each other, because each of them claims, in a sense, to cover the whole field, that is, to interpret all experience from its own point of view. Philosophy tries to mediate between them,

and the task has so far been beyond its powers. Some of the new philosophies undermine the authority of science, as some of the older systems undermined the authority of religion. Complete reconciliation is not in sight; but there is no reason for hostility, which reacts unfavourably upon our whole view of life. For the eternal Values are not entirely separate from each other."

NOMOGENESIS *or Evolution Determined by Law.*

By Leo S. Berg. Introduction by D'Arcy W. Thompson. Translated from the Russian by J. N. Rostovtsow. *Constable and Co.*
28 shillings *London*
$8\frac{1}{2} \times 5\frac{1}{2}$; xviii + 477

This is orthogenesis all over again. To the author "evolution is in a great measure an unfolding of existing rudiments." The "fundamental property of the living 'being' is purposive structure." But how the "purposive structure" came to be so is not explained. Berg takes it as axiomatic, and deduces from it support for Lamarck and rejection of Darwin. Philosophically the book is not very penetrating. Biologically it contains a lot of interesting observations and discussions. It has a bibliography of 20-odd pages, and a detailed index.

SELECTED ARTICLES ON EVOLUTION.
Compiled by Edith M. Phelps.
The H. W. Wilson Co.
\$2.40 $8 \times 5\frac{1}{2}$; liii + 283 *New York*

This book is neutral. Biologists and fundamentalists are each allowed their say, in the form of quotations. It is essentially a book of the "debater manual" type, from which the superficial and hurried student can get "something on both sides." To the biologist it will chiefly be useful in collecting in one volume some choice fundamentalist tidbits where he can find them easily. The editing is well done.

AUTHORITATIVE STATEMENTS ON SCIENCE, EVOLUTION, RELIGION AND THE BIBLE.
Compiled by Samuel S. Wyer. *S. S. Wyer.*
1014 Hartman Bldg., Columbus, O.
9×6; 31 (paper)

Another reconciliation document by a consulting engineer, consisting of some 25 pages of short quotations from 41 bibliographically cited authorities, with Lyman Abbott heading the list and Albert E. Wiggam ending it. There is a laudatory introduction by President W. O. Thompson of Ohio State University. It is entertaining to see science overtly espousing authoritarianism as its ultimate controversial method. How the Jesuit theologians must be chuckling!

EVOLUTION.
By J. Graham Kerr. *The Macmillan Co.*
\$3.50 9×6; x + 278 *New York*

An elementary treatise on organic evolution for the beginner in science and the general reader. The author is Regius Professor of Zoology at Glasgow. The treatment of the old material and arguments is carried out in a refreshingly vigorous and unhackneyed way, in part because emphasis is placed throughout on the importance of old-fashioned field natural history as the groundwork of knowledge of evolution.

GENETICS

CONTRIBUTIONS TO A KNOWLEDGE OF INHERITANCE IN MAMMALS. *I. Studies of Color Inheritance and of Linkage in Rabbits, by W. E. Castle. II. Fertility and Sterility in the Norway Rat, Mus norvegicus, by Horace W. Feldman. III. The Japanese Waltzing Mouse: Its Origin, Heredity and Relation to the Genetic Characters of Other Varieties of Mice, by William H. Gates. (Publication No. 337.)*

Carnegie Institution of Washington
$1.50 *Washington, D. C.*
$6\frac{3}{4}$ x 10; 138 + 14 plates (paper)

All three of these papers are important contributions to genetics. Castle concludes that in rabbits "the factors Dutch, English and Angora are linked; their genes lie in one chromosome, probably in the order named. Only 0.1 per cent of crossing-over has been observed between Dutch and English but each of these genes shows crossing-over with Angora in a frequency of 12 to 14 per cent. The only other positively demonstrated linkage in rabbits is between the color-factor and its allelomorphs on one hand and black *vs.* brown on the other hand. Both these genes lie in the same chromosome and the cross-over percentage between them is 34.6 ± 1.0. No positive evidence has been obtained of a difference in rate of crossing-over between the two sexes in rabbits, though such a difference is known to occur in rats and mice. The nine unifactorial characters of rabbits discussed in this paper, as indicated by their linkage relations, lie in 6 different chromosome pairs, only 2 of which contain more than one known gene."

Gates' interesting study of the Japanese waltzing mouse leads to the following conclusions: "That the pure race of Japanese waltzing mice has been derived from the wild form, *Mus wagneri*, and that the varietal name of *Mus wagneri rotans* Fortuyn is therefore valid. That in interspecific crosses of animals (mice) as in plants, there is a tendency for each set of parental chromosomes to group together, forming associate systems which may materially modify Mendelian ratios. That interspecific hybrids in mice exhibit heterosis to a marked degree as to size, vitality, longevity, and metabolic and reproductive activities. That the factor for waltzing is neither sex-linked nor linked with the factors for agouti, albinism, pink-eye, dilution, brown, Dutch spotting, short-ear or kinky-tail. Waltzing shows no evidence of association with any lethal factor. That the character, kinky-tail, is definitely linked, either genetically or physiologically, with short-ear."

THE PHYSIOLOGY OF THE CONTINUITY OF LIFE.

By D. Noël Paton. *The Macmillan Co.*
$4.00 $8\frac{1}{2}$ x $5\frac{1}{2}$; x + 226 *New York*

This is a poor book. The author, who is a human physiologist, takes as his motto *Jurare in verbis nullius magistri*. This is a noble and altogether praiseworthy sentiment. But the author makes it the excuse to dismiss as worthless or dubious about all of the most solidly established facts and ideas of modern genetics, and to accept with laudation a good part of the most arrant quackery and pseudo-science which biology has achieved in the last quarter-century. Much of the book deals with material with which the author has no first hand familiarity. The result is sad. And in detail the writing is carelessly done. The distinguished Dutch botanist masquerades under the cognomen "Von Vries." Only the context enables the informed reader to recognize that by "Rotier" is meant rotifer. The book is a

fine example of the folly of a specialist in one field of science trying to expound critically the highly technical results of another.

HEREDITY. *Fifth Edition, Thoroughly Revised.*
By J. Arthur Thomson. *R. V. Coleman*
$5.00 *(522 Fifth Ave.) N. Y.*
$8\frac{1}{4}$ x $5\frac{1}{2}$; xiv + 542

To what was in former editions this revision adds some of the newer results in the field of genetics. But the general point of view seems, on the whole, a bit old-fashioned. Perhaps it is a good thing to have such a book available, in which a wise, mature and philosophical general biologist, who is not a specialist in genetics, reviews in a detached way the whole field. But he does incorporate some dreadful bunk from the literature, without any indication that his critical blood-pressure has been elevated in the least.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 204.* Containing following articles: *Züchtung der Homopteren*, by Carl Börner; *Züchtung von Neuropteren, Trichopteren und Panorpaten (Mecopteren)*, by Franz Heikertinger; *Züchtung der Lepidopteren*, by E. Fischer; *Züchtung von Dipteren*, and *Züchtung von Coleopteren*, by Franz Heikertinger; *Züchtung von Hymenopteren*, by Josef Fahringer.
Urban und Schwarzenberg
12.30 marks 7 x 10; 270 (paper) *Berlin*

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 207.* Containing following articles: *Züchtung von Ameisen*, by Heinrich Kutter; *Haltung und Zucht der Honigbiene*, by Max Hartmann; *Die Zucht des chinesischen Seidenspinners (Bombyx mori)*, by Herbert Michael; *Methoden zum Züchten von Landpulmonaten*, by Karl Künkel; *Pflege und Zucht weiterer wirbelloser Landtiere*, by Paul Kammerer; *Methoden der biologischen Bekämpfung schädlicher Insekten im Pflanzenschutz*, by F. Stellwaag. *Urban und Schwarzenberg*
8.40 marks 7 x 10; 486 (paper) *Berlin*

These two numbers of the Abderhalden handbook are of particular interest to geneticists, giving practical directions for cultural procedures.

GENERAL BIOLOGY

ON THE TRAIL OF ANCIENT MAN. *A Narrative of the Field Work of the Central Asiatic Expeditions.*
By Roy Chapman Andrews (with an introduction and chapter by Henry Fairfield Osborn).
G. P. Putnam's Sons
$6.00 $6\frac{1}{4}$ x $9\frac{1}{4}$; xxiv + 375 *New York*

The real romance of biology is in the field and not the laboratory. The achievements of the field naturalist are usually not so spectacular as those of the laboratory worker, though dinosaur eggs do produce a thrill if earnestly thought about. But the explorer does have a lot of fun along with and out of his proper work. This beautifully printed and illustrated volume gives a popular account of the Central Asiatic Expeditions of the American Museum of Natural History. Roy Chapman Andrews is a superb story-teller, as well as organizer and administrator. The person who does not get a thrill out of this book should consult a physician. Something is surely wrong with him. The title is a little misleading. So far the Expeditions have had no great luck with ancient man. But they are on the trail and the by-products are sufficiently exciting and important to justify more than one book.

DIE ANORGANISCHEN GRENZGEBIETE DER BIOLOGIE (*insbesondere der Kristallvergleich*).
By Hans Przibram. *Gebrüder Borntraeger*
7.50 marks $8\frac{3}{4} \times 5\frac{1}{2}$; 240 *Berlin*

An interesting review of the literature regarding the behavior of crystals, particularly in respect to growth and regeneration after removal of parts. The discussion is from the point of view of a biologist, who has himself done a good deal of original research in these fields of crystallography. The result is a serious and significant evaluation of the analogies between inorganic and organic behavior. There are 65 illustrations, a bibliography covering 23 pages, and a detailed index.

CUVIER ET LA SCIENCE DE LA NATURE.
By Louis Roule. *Ernest Flammarion*
9 francs $4\frac{3}{4} \times 7\frac{1}{4}$; 246 (paper) *Paris*

This portion of the author's interesting attempt to write the history of biology around the lives of the great French naturalists is a useful and well-written contribution to the literature of the history of science. It is divided into three parts, of which the first is biographical; the second an analysis of Cuvier's writings; and the third an evaluation of the influence of Cuvier upon the current of biological thought, especially with reference to organic evolution. The author is professor at the Museum of Natural History.

BIOLOGY. "*Science for All*" *Series.*
By O. H. Latter. *John Murray*
3s. 6d. $7\frac{1}{2} \times 5$; vii + 197 *London*

Mr. Latter is well known as a successful teacher of biology. This little elementary text of general biology, with simple laboratory directions following each chapter, will be found by American teachers to contain many suggestive ideas likely to be useful in their work.

PROTOPLASMA. *Internationale Zeitschrift für Physikalische Chemie des Protoplasten. Band 1, Heft 1.* *Gebrüder Borntraeger*
14 marks *Berlin*
$7\frac{1}{4} \times 10\frac{1}{4}$; iv + 176 (paper)

Specialization and differentiation in the biological disciplines grows ever finer. The Quarterly Review of Biology heartily welcomes this new-comer to the widening family of special journals. It is to concern itself with the physiology of protoplasm, looked at as a physico-chemical system. Competent editors and associates guarantee its scientific soundness. We wish *Protoplasma* all success.

AN INTRODUCTION TO BIOLOGY.
By Alfred C. Kinsey. *J. B. Lippincott Co.*
\$1.68. $7\frac{3}{4} \times 5\frac{1}{4}$; xiv + 558 *Philadelphia*

This new high school text for courses in general biology is especially noteworthy for its illustrations. While mainly garnered from existing sources the author has shown much originality and freshness of viewpoint in their assembling. We commend this book to the attention of teachers.

WERK UND WIRKUNG. *Eine Vortragsreise. (Moderne Biologie Heft 11.)*
By Prof. Dr. Hans Much. *Curt Kabitzsch*
7.20 marks $7\frac{1}{2} \times 5$; 227 (paper) *Leipzig*

A series of lectures on various medical and biological-philosophical subjects given by the author, who is a professor at

Hamburg, in Budapest, Pecs, Agram, Barcelona, Madrid, and Davos. There is some interesting, and in part original, philosophical speculation in the book.

THEORETICAL BIOLOGY.

By J. von Uexküll. *Harcourt, Brace and Co.*
$5.50 $8\frac{1}{2} \times 5\frac{1}{2}$; xvi + 362 *New York*

It is a useful thing to have Baron von Uexküll's well-known treatise on theoretical biology translated into English. Biologically his position is vitalistic. Philosophically he derives from Kant, and ends in a position which has some points of resemblance to that of Whitehead. The value of the book is impaired by the absence of an index.

GOLDFISH CULTURE FOR AMATEURS. *How to Breed and Rear Goldfish in Aquaria and Ponds.*

By A. E. Hodge and Arthur Derham.
Frederick A. Stokes Co.
$1.50 $5\frac{1}{4} \times 7\frac{3}{4}$; xi + 103 *New York*

A thoroughly practicaly little treatise. The authors speak with the authority of first-hand-experience. It is entertaining to know that Epsom salts, that noble therapeutic agent, will cure goldfish of dyspepsia.

DIE EXISTENZGRÜNDE DER ZELLBILDUNG UND ZELLTEILUNG, DER VERERBUNG UND SEXUALITÄT. *Untersuchungen aus dem Gebiete der exakten Biologie.*

By Victor Schiffner. *Gustav Fischer*
7.50 marks *Jena*
$6\frac{1}{4} \times 9\frac{1}{4}$; v + 160 (paper)

A philosophical and metaphysical discussion of the data of biology, leading to a pronounced mechanistic position.

HUMAN BIOLOGY

THE UPPER PALAEOLITHIC AGE IN BRITAIN.

By D. A. E. Garrod.
Oxford University Press
$3.50 9 x 6; 211 *New York*

Miss Garrod has done a useful service in bringing together, with abundance of illustrations, all that is known regarding the presence of later paleolithic man in England. The work is honored by an introduction from the pen of M. l'Abbé Henri Breuil, whose pupil Miss Garrod was. The general conclusions are:

> We see this country as the Ultima Thule of Upper Palaeolithic Europe, a north-west cape, remote and inhospitable, bounded by the great ice-sheet under which Scotland and Ireland still lay buried. As we should expect, traces of human occupation are scarce, but we can make out the same general succession of industries as in other parts of western Europe, with certain gaps and certain variations.
>
> The most abundant remains are of the Aurignacian, and its Middle, or 'Typical,' phase as represented at Paviland, does not differ essentially from that of France and Belgium. In Upper Aurignacian levels, however, traces of a distinct local facies begin to appear in the shape of semi-geometrical forms, derivatives of the Gravette point, of which the most characteristic is an elongated trapeze (Paviland, Langwith, Creswell Crags). At the same time the proto-Solutrean point retouched on the bulbar face, which in France and Belgium occurs in the Font-Robert level, that is, at the very end of the Aurignacian, shows a special development.
>
> From this point onwards the English record grows obscure. As we have seen the increased cold of late Upper Palaeolithic times brought about a return of arctic conditions and industrial remains are rare.

NOTES ON DEMOCRACY.

By H. L. Mencken. *Alfred A. Knopf, Inc.*
$2.50 $4\frac{1}{4} \times 7\frac{1}{2}$; v + 212 *New York*

U. S. A SECOND STUDY IN DEMOCRACY.

By H. E. Buchholtz. *Warwick and York, Inc.*
$2.20 $7\frac{1}{2} \times 5$; ix + 400 *Baltimore*

These two books cover the same ground in many respects. Taken together they furnish a devastating criticism of democracy. Mr. Buchholz demolishes it as practised, and Mr. Mencken both in practise and in theory. The latter stops at that point, and offers no guaranteed curative eye-water. Mr. Buchholz is bolder. He has a scheme to make democracies function better. But its efficacy is open to debate. His plan, from a detached viewpoint, has a suspicious likeness to the activities of the Anti-Saloon League. It seems to add one more brand of uplift to the already considerable number which annoy intelligent people. But perhaps it is along that pathway that evolution will choose to go. Mr. Mencken's book, beyond exhibiting his superb literary talents at their very best, is perhaps the most important contribution to the world's intellectual resources that he has yet made, not excepting *The American Language*. We welcome both books as valuable additions to the literature of human biology.

DIE MENSCHLICHEN SKELETRESTE AUS DER STEINZEIT DES WAUWILERSEES (LUZERN), *und ihre Stellung zu anderen anthropologischen Funden aus der Steinzeit*.
By Otto Schlaginhaufen. *Eugen Rentsch*
19 francs (Swiss) *Erlenbach-Zürich*
$10\frac{3}{4}$ x 8; 278, 12 plates (paper)

A thorough metrical study of six finds of skeletal remains of prehistoric man, by the Director of the Anthropological Institute of the University of Zürich. The bones came from an old lake bed in *Kanton Luzern*. The material consists of (1) the skeleton of a woman about 30 years old and only 142.3 cm. in height. (2) A left femur. (3) A left os calcaneus. (4) A group of bones consisting of a left humerus, two defective pelvic blades, and a left femur. (5) A group of defective bones, including a skull cap. (6) A left parietal bone. It is all apparently neolithic. The volume is beautifully printed, contains an extensive bibliography, and a detailed index, and besides the text figures is illustrated with 12 superb photogravure plates. Altogether it is a substantial contribution to the technical literature of anthropology.

UNGARISCHE BIBLIOTHEK III. 2, *Bibliographia Hungariae. II. Geographica. Politico-oeconomica. Verzeichnis der 1861–1921 erschienenen, Ungarn betreffenden Schriften in nichtungarischer Sprache.*
Edited by Robert Gragger.
Walter de Gruyter und Co.
22 marks *Berlin and Leipzig*

Whatever biological interest this bibliography of literature about Hungarian geography and political economy may have derives from the fact that both subjects are looked at broadly, and there is a good deal of useful anthropological and statistical material noted.

GRUNDRISS DER ANTHROPOLOGIE.
By M. W. Hauschild. *Gebrüder Borntraeger*
10.50 gold marks *Berlin*
$6\frac{1}{4}$ x 10; viii + 235 (paper)

This book is only the first draft of what the author intended to be a much more extensive work. But his untimely death from malaria, contracted on a scientific expedition in Java, prevented the carrying out of the larger plan. The smaller work, as he left it, has been edited and prepared for the press by Professor Eugen Fischer. It is a treatise on physical anthropology, written from the viewpoint

of a trained anatomist. It does not deal systematically with the different races of men, but rather discusses the anatomy and biology of those human structures which are anthropologically important. It will interest and stimulate the general biologist more than most anthropological treatises.

THE HUMAN BODY.
By Marie Carmichael Stopes.
G. P. Putnam's Sons
$2.50 *New York*
$5\frac{1}{4}$ x 8; viii + 268 + 7 plates

The versatile and accomplished Dr. Stopes has now written a little treatise on elementary human anatomy and physiology. The depth of its philosophy is indicated by the following account of the liver:

> The liver is one of the largest and heaviest organs in the body and its dark crimson texture is both soft and firm, the cells richly packed with food material and the whole interspersed with fine ramifications of the blood vessels. The old phrase: 'Is life worth living—All depends on the liver' has a great deal of truth in it in its purely materialistic sense, and those who are 'liverish,' whose liver and bile ducts do not act properly, suffer many of the minor inconveniences which go with indigestion and that uncomfortable feeling of swimminess in the head which precedes sickness.

There are six colored anatomical charts at the end, besides numerous text illustrations.

FROM TRIBE TO EMPIRE. *Social Organization among Primitives and in the Ancient East.*
By A. Moret and G. Davy. Alfred A. Knopf
$6.00 $9\frac{1}{8}$ x $6\frac{1}{8}$; xxx + 371 *New York*

In this valuable contribution to the series *The History of Civilization* a historian and a sociologist collaborate in an attempt to trace the origin of political organization. In Egypt prior to 4000 B. C. the social organization was that of clans, which the authors find to be the first social organization among uncivilized peoples, rather than the family. About 3300 B. C. Menes founded the centralized monarchy and established the divine right of kings. The historical records of Egypt, Chaldea, and the Near East generally, enable the authors to trace the actual political development up to the firmly established empire. There is a bibliography, and an index.

PRÉHISTOIRE DE LA NORVÉGE.
By Haakon Shetelig.
Harvard University Press
$1.85 $7\frac{3}{4}$ x $5\frac{1}{4}$; 280 (paper) *Cambridge*

An interesting, scholarly résumé of the results of archeological research in Norway, starting with the Old Stone Age and coming down to the Vikings. The book is beautifully printed, and illustrated with half-tone plates. There is a bibliography covering some eleven pages, and a detailed index.

OUR PREHISTORIC ANCESTORS. *The Story of Man's Evolution to the End of the Old Stone Age.*
By Dorothy Davison. Methuen and Co., Ltd.
7s. 6d. 5 x 7; xiv + 208 *London*

A popular and derivative account of early man, and his artefacts. The author adopts the views of Professor Elliot Smith on most controverted points. The book is extensively and rather attractively illustrated with line drawings. It is written in a pleasant, easily readable style.

MODERN SCIENCE AND PEOPLE'S HEALTH.

Edited by Benjamin C. Gruenberg. Contributing Authors: Charles R. Stockard, Hugh S. Taylor, Walter H. Eddy, William A. White, C. E. A. Winslow, Haven Emerson.

W. W. Norton and Co.

\$2.50 $5\frac{1}{2} \times 8\frac{1}{2}$; vi + 250 *New York*

A high-toned contribution to the uplift. Dr. Gruenberg is a competent editor and has kept the amount of pious exhortation at a minimum and the well-written, sound science at a maximum. We congratulate him on producing so interesting a book, and driving so successfully a six-handed team of mettlesome scientists. The topics discussed, after Dr. Gruenberg's introductory essay about science in a democracy, are: Heredity and environment (Stockard); biological chemistry (Taylor); nutrition (Eddy); psychiatry (White); preventive medicine (Winslow); public health (Emerson).

ZOOLOGY

PROTOZOOLOGY. *A Manual for Medical Men, Veterinarians and Zoologists. Volumes I and II.*

By C. M. Wenyon. *William Wood and Co.*

\$25 per set $9\frac{1}{2} \times 6\frac{1}{2}$; xvi + 1563 *New York*

This is a monumental treatise. It aims to cover the whole field of protozoology, but designedly the free-living forms are discussed only briefly while the parasitic forms are treated in great detail, and with a wealth of illustrations. This book, taken with Calkins' *Biology of the Protozoa*, recently noticed in these pages, furnishes the zoologist with a thorough, critical, up-to-date résumé of the present state of knowledge of the biology of the protozoa. Wenyon's wide experience as a medical zoologist enables him to speak with first hand authority about the parasitic protozoa. But his viewpoint throughout holds fast to the sound anchor of general biology. He says:

> The student of the Protozoa which are pathogenic to man and domestic animals should have a sound knowledge of other parasitic Protozoa, and at least a good working knowledge of non-parasitic forms as well. Conversely, those who study free-living Protozoa should have a clear conception of the parasitic forms, for the extensive investigations of recent years have contributed so much to our knowledge that in many respects they are better known than their free-living relations, particularly as regards the completeness of their life-histories and the probable course of their evolution.

There is a very extensive bibliography, covering 98 pages of fine print, and a detailed index, covering nearly 50 pages. Altogether this is a substantial and welcome contribution to the literature of zoology.

THE NATURAL HISTORY OF ANTS. *From an Unpublished Manuscript in the Archives of the Academy of Sciences of Paris. By René Antoine Ferchault de Réaumur. Translated and Annotated by William Morton Wheeler.* *Alfred A. Knopf*

\$5.00 $9\frac{1}{2} \times 6\frac{1}{4}$; xvii + 280 *New York*

Professor Wheeler has performed a very valuable service in bringing to light this memoir on ants by the great naturalist Réaumur and making it available for present day students. The manuscript has hitherto been lying unpublished in the archives of the Academy. In this beautifully printed volume the French text is given in full, prefaced by a biographical sketch of Réaumur and followed by Professor Wheeler's translation of it into English, and his extensive annotations. It is a superb piece of scholarly work, done in a manner that no one but Wheeler could achieve. All biologists will welcome it as an important contribution to the history of science.

ARISTOCRATS OF THE AIR.
By Capt. C. W. R. Knight, and a Preface by Viscount Grey of Fallodon.
Frederick A. Stokes Co.
$7.50 10 x $7\frac{1}{2}$; xii + 166 *New York*

Capt. Knight is a keen ornithologist, who brings together in this book a series of superb photographs, illustrative particularly of the nesting habits of some of the rarer British birds of prey, along with an entertaining textual account of his observations of these birds. Interesting and valuable records are given of a family of Montagu's harriers, of a heronry, and of a shelduck's nest, among others. The value of the book from a zoological viewpoint would have been enhanced if scientific names had been given along with the common names. In the last chapter the author gives a brief account of the training of hawks for "the sport of kings"—falconry—at which he is an expert.

INSECTS OF WESTERN NORTH AMERICA. *A Manual and Textbook for Students in Colleges and Universities and a Handbook for County, State and Federal Entomologists and Agriculturists as well as for Foresters, Farmers, Gardeners, Travelers, and Lovers of Nature.*
By E. O. Essig. *The Macmillan Co.*
$10.00 6 x $9\frac{1}{4}$; xi + 1035 *New York*

This is a working manual of general entomology, abundantly and well illustrated. It will be widely useful as a reference work, since it will serve as a sort of colossal index to insects and the literature about them. Covering the whole field taxonomically as the book does, though limited geographically, descriptions are necessarily brief and keys go generally only to families. From an editorial point of view the tremendous amount of detailed work which the book represents has been extremely well done.

THE PLANT LICE OR APHIDIDAE OF GREAT BRITAIN. *Vol. I.*
By Fred V. Theobald. *Headley Bros.*
25 shillings *London*
$8\frac{3}{4}$ x $5\frac{1}{4}$; ix + 372 (paper)

The first volume of a useful systematic monograph on the aphids, by the leading British authority on the group. The description of each form is followed by an account of what is known regarding its life history. The volume opens with a brief account of the external anatomy, and the general biology of aphids. The taxonomic portion is well illustrated with line drawings, which will be of material help in identification.

HOW INSECTS LIVE. *(An Elementary Entomology.)*
By Walter H. Wellhouse.
The Macmillan Co.
$5.00 $5\frac{3}{4}$ x $8\frac{1}{4}$; xv + 435 *New York*

This excellent elementary textbook by the associate professor of entomology at Iowa State College, after first describing briefly the essentials of insect anatomy and physiology, devotes a series of chapters to more detailed accounts of each order of insects. At the end of the book is a chapter on collecting with a key to the orders and families. The book is well illustrated and indexed, and gives brief bibliographical lists at the end of each chapter.

MAMMUTLEICHEN UND URWALDMENSCHEN IN NORDOST-SIBIRIEN.
By E. W. Pfizenmayer. *F. A. Brockhaus*
M. 14 6 x 9; 341 *Leipzig*

This is an interesting and well illustrated popular account of two expeditions, sent by the St. Petersburg Academy of Sciences in 1901–2 and 1908 to North

Siberia in search of mammoth remains. The sensation caused by the finding of the Beresowka specimen with skin and many soft parts intact and capable of histological study will be recalled. The long delay in the publication of the book is the result of a series of misfortunes which befell the author, in which the World War is included. But belated as it is the book is well worth reading. It contains a good many interesting anthropological and ethnological observations.

THE NEW NATURAL HISTORY. *Volumes II and III.*
By J. Arthur Thomson. G. P. Putnam's Sons
$6.00 each volume *New York*
8 x 10½; Vol. II, 383
Vol. III, xiv + 383

These two volumes maintain the high standard set in the first volume of this popular natural history, in respect of both text and illustrations. Professor Thomson has no present peer as a writer of popular biology. The chapter on "Life-Histories" in the second volume, and that on "Animals and Man" in the third are especialy worthy of praise. Father, even though he be a professional biologist, should not leave the reading of these chapters entirely to the children.

DIE ÖKOLOGIE DER BLATTMINIERENDEN INSEKTENLARVEN. (*Zoologische Bausteine, Band 1, Heft 2.*)
By Martin Hering. Gebrüder Borntraeger
18 marks 6¾ x 10; 254 (paper) *Berlin*

This memoir includes the general biological portion of a comprehensive memoir on the leaf mining insects, which is projected by the author, who is a staff member of the Zoological Museum at Berlin. It is a thorough review of the literature on the ecological and general biological side, grounded upon the author's extensive personal researches in the field. There is a bibliography covering nineteen pages, an excellent index, and two plates. It is a valuable addition to the literature.

DIE TIERWELT DER NORD- UND OSTSEE. *Lieferung IV, Lieferung V.*
Edited by G. Grimpe and E. Wagler.
Akademische Verlagsgesellschaft M. B. H.
Mk. 18 8½ x 6 *Leipzig*
Mk. 8.80 Lieferung IV, 250 (paper)
Lieferung V, 116 (paper)

These two numbers in this monograph of the North Sea fauna, previous parts of which have been noticed in earlier numbers of THE QUARTERLY REVIEW OF BIOLOGY, cover the following subjects: Bryozoa, by E. Marcus; Fishes, general part, by H. M. Kyle and E. Ehrenbaum; Teleostei Physoclisti, by G. Duncker and Erna W. Mohr; Lamellibranchia, by F. Haas; and Copelata, by A. Bückmann. An excellent standard of quality is maintained throughout.

NOTES ON THE GAME BIRDS OF KENYA AND UGANDA. (*Including the Sand-Grouse, Pigeons, Snipe, Bustards, Geese, and Ducks.*)
By Sir Frederick J. Jackson.
Williams and Norgate, Ltd.
25 shillings 9 x 6; xv + 258 *London*

An interesting contribution to local ornithology covering systematically the groups and territory indicated by the title. The illustrations are in the form of colored plates reproduced by color printing from usually lithographic originals published elsewhere. The synonymy is given for each species, a brief description, and notes on habits and

habitats. Curiously enough, considering the character of the book, there is no index.

BRITISH SNAILS. *A Guide to the Non-Marine Gastropoda of Great Britain and Ireland Pliocene to Recent.*
By Arthur Erskine Ellis.
Oxford University Press
10 shillings *Oxford*
$7\frac{3}{4} \times 5$; 275 + 14 plates

A taxonomic manual of the land and freshwater molluscs of the British Isles. The more common species are figured on 14 photogravure plates. Brief notes on habits, habitat, and geographical distribution follow each diagnosis. The work is carefully done. It is a useful handbook for the field naturalist. In a good many cases the original description is quoted *verbatim.*

THE HOUSE-FLY. *Its Life History, Importance as a Disease Carrier, and Practical Measures for its Suppression. (Economic Series No. 1A.)*
By E. E. Austen.
British Museum (Natural History)
1 shilling $5\frac{1}{2} \times 8\frac{1}{4}$; 68 (paper) *London*

The second edition of a well written and illustrated popular monograph on *Musca domestica*, in which special attention is given to means of suppression.

ZOOLOGIE IM GRUNDRISS.
By Walter Stempell. *Gebrüder Borntraeger*
10,50 marks *Berlin*
Lieferung 4, $7\frac{1}{8} \times 10\frac{1}{2}$; xx + 212 (paper)

Brings to a close an excellent general zoology, of which the earlier parts have been noticed in previous numbers of The Quarterly Review of Biology.

A GENERAL CONSIDERATION OF SNAKE POISONING AND OBSERVATIONS ON NEOTROPICAL PIT-VIPERS. *Contributions from the Harvard Institute for Tropical Biology and Medicine, II.*
By Afranio do Amaral.
Harvard University Press
\$2.50 *Cambridge*
$10\frac{1}{2} \times 7\frac{1}{2}$; 64 + 16 plates

The first 18 pages of this monograph deal generally with snake poisoning, while the remainder of the book concerns itself with taxonomic matters pertaining to various species of *Bothrops*. The work was done under the direction of Dr. Thomas Barbour, which ensures its soundness. It is illustrated with 16 plates, mostly colored.

INSTRUCTIONS FOR COLLECTORS: *No. 7—Blood-Sucking Flies, Ticks, etc.*
By E. E. Austen.
British Museum (Natural History)
Sixpence $5\frac{1}{2} \times 8\frac{1}{4}$; 28 (paper) *London*

Brief descriptions of the appearance and habits of blood-sucking flies other than mosquitoes, with detailed directions for collecting and forwarding such animals to England. There is also a section on collecting fleas, bugs, lice, ticks and smaller mites.

A SYNOPSIS OF THE FAMILIES AND GENERA OF NEMATODA.
By H. A. Baylis and R. Daubney.
British Museum (Natural History)
10s. 6d. *London*
$5\frac{3}{4} \times 8\frac{3}{4}$; xxxvi + 277

An excellent taxonomic monograph including all the genera of nematodes described prior to the end of the year 1923. The freeliving and parasitic nematodes are

here united in a common system of classification. It seems a pity that there are no illustrations whatever.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 199.* Containing following articles: *Methoden zur Erforschung des Vogelzuges*, by J. Thienemann; *Methoden zur Behandlung der Atemphysiologie der Insekten*, by Albert Koch; *Die Verfahren zur Erforschung der Tierfluges*, by Oskar Prochnow.

Urban und Schwarzenberg
7.50 marks 7 x 10; 172 (paper) *Berlin*

The first paper in this number of the Abderhalden handbook is brief, and deals with methods of bird banding, etc., in connection with the study of migration. The second paper on the respiration of insects is an important and valuable one. So also is the last on animal flight.

A LABORATORY MANUAL FOR ELEMENTARY ZOOLOGY.
By Libbie Henrietta Hyman.
University of Chicago Press
$2.50 10 x 7; xviii + 182 *Chicago*

The second edition of the laboratory manual used for a number of years in the beginning zoology course at the University of Chicago. The directions are very detailed, a procedure which is ably defended by the author in the preface.

SYNONYMY OF THE BRITISH NON-MARINE MOLLUSCA. (*Recent and Post-Tertiary*) *Compiled and annotated by A. S. Kennard and B. B. Woodward.*
British Museum (Natural History)
£1 $5\frac{1}{2}$ x $8\frac{3}{4}$; xxiv + 447 *London*

A detailed, critical compilation of the synonomy of the British species of land and fresh water molluscs, of interest and usefulness to taxonomic malacologists.

BOTANY

WILHELM HOFMEISTER. *The Work and Life of a Nineteenth Century Botanist. Ray Society Volume No. 111.*
By K. von Goebel. Translated into English by H. M. Bower and edited botanically by F. O. Bower. *Dulau and Co., Ltd.*
12s. 6d. $8\frac{3}{4}$ x $5\frac{1}{2}$; xi + 202 *London*

For many years the Ray Society has performed the useful service of issuing annually one or two important zoological or botanical monographs, usually taxonomic in character, but with the occasional interpolation of an important biographical memoir. This memoir of Hofmeister by Goebel, his last surviving pupil, is a valuable contribution to the history of science. Goebel devotes this part of the book to a critical exposition of the significance to the development of biology of his master's work. This is followed by an appendix of some fifty odd pages, in which is given a simple and rather charming account of Hofmeister's life, written by his daughter, Frau Constanze Ganzenmüller.

DIE PFLANZENAREALE. *Sammlung kartographischer Darstellungen von Verbreitungsbezirken der lebenden und fossilen Pflanzen-Familien, -Gattungen und -Arten. 1 Reihe, Heft 1, und Heft 2.*
Edited by E. Hannig, H. Winkler, Ludwig Diels and G. Samuelsson. *Gustav Fischer*
7.50 marks each 13 x 12 *Jena*
Heft 1, iii + 14 + 10 maps (paper)
Heft 2, 16 + 10 maps (paper)

These first two numbers of an undertaking, which if realized will be extremely useful to all students of evolution, are excellently done. The maps are well printed and the indications of distributional areas are beautifully clear. Their critical accuracy is guaranteed by the fact that each group is handled by a specialist. The authors and groups mapped in these two numbers are as follows: A. Engler, *Saxifraga* I; F. Pax, *Acer* I; L. Diels, *Casuarina;* F. Vierhapper, *Soldanella;* M. Rikli, *Pinus pinea;* E. Hannig, *Genista anglica;* Hub. Winkler, Musaceae; F. Pax, *Sapium;* J. Mattfeld, European species of *Abies;* L. Lämmermayr, *Fagus silvatica* and *Fagus orientalis;* E. Hultén, *Pinus pumila* and *Hierochloë pauciflora.*

GENERAL BOTANY. *With Special Reference to its Economic Aspects.*
By C. Stuart Gager.
P. Blakiston's Son and Co.
\$4.00 $8\frac{1}{2}$ x $5\frac{3}{4}$; xvi + 1056 *Philadelphia*

This is an excellent textbook of general botany of college and university grade. Written out of wide knowledge and sound judgment it seems likely to have a large field of usefulness. Three chapters on plant genetics are contributed by Dr. O. E. White. There are 689 illustrations, a detailed index, and abundant documentation of the literature. Altogether it is a first-rate piece of textbook writing.

MANUAL OF PLANT DISEASES.
By Frederick DeF. Heald.
McGraw-Hill Book Co.
\$7.00 6 x 9; xiii + 891 *New York*

A comprehensive general text book of plant pathology, which attempts to cover the whole field, including plant diseases due to direct environmental injuries, as well as those caused by bacteria, fungi, and filterable viruses. The discussion of each disease is followed by a brief bibliography of the important literature on it. The book is well illustrated and indexed. It is a valuable addition to the text book literature.

PFLANZEN-PHYSIOLOGISCHE STUDIEN.
By Rose Stoppel. *Gustav Fischer*
7.50 marks $6\frac{1}{2}$ x $9\frac{1}{2}$; 165 (paper) *Jena*

The purpose of the author of this volume, who is a *Privatdozent* at the University of Hamburg, is to act as a *liaison* officer between the plant physiologists, on the one hand, and the animal physiologists and medical men, on the other hand. The book gives a brief *résumé* of the present status of plant physiology, under the following heads: Respiration, fermentation, narcosis, photodynamic sensitization, chlorophyll, assimilation of carbon dioxide, transpiration, water absorption and conduction, growth, geotropism, phototropism, conduction of stimuli, periodic phenomena. The book is well written, and is interesting, but suffers from the lack of an index, and of illustrations.

A MONOGRAPH OF THE BRITISH LICHENS. (*A Descriptive Catalogue of the Species in the Department of Botany, British Museum.*) *Part II.*
By Annie L. Smith.
British Museum (Natural History)
20 shillings *London*
$8\frac{3}{4}$ x 6; ix + 447; 63 plates

A second, revised, edition of Part II of this standard handbook on the taxonomy of the lichens. The plates are excellent for purposes of identification.

CARGOES AND HARVESTS.
By Donald C. Peattie. D. Appleton and Co.
$2.50 $8\frac{1}{4} \times 5\frac{1}{4}$; 311 *New York*

An interesting popular account, well written and quaintly illustrated, of the history of agricultural exploration, and of the development of plant products for the use of man. There are useful brief bibliographies following each chapter, and a detailed index.

FIELD MANUAL OF TREES. *Including Southern Canada and the Northern United States to the Southern Boundary of Virginia, Kentucky and Missouri Westward to the Limits of the Prairie. Third Edition.*
By John C. Schaffner. R. G. Adams and Co.
$1.50 $7 \times 4\frac{1}{2}$; 154 *Columbus, O.*

The third edition of a useful little determinative manual for the trees of the Northern United States and Southern Canada, by the professor of botany at Ohio State University.

PLANTS AS INVENTORS.
By R. H. Francé.
Simpkin, Marshall and Co.
1 shilling $7\frac{3}{4} \times 5\frac{1}{4}$; 63 *London*

An entertaining little popular book showing how the essential elements of man-invented mechanisms are found duplicated in living things, particularly plants.

UNTERSUCHUNGEN ÜBER MARCHANTIACEEN. *Botanische Abhandlungen, Heft 10.*
By Dr. E. Bergdolt. Gustav Fischer
4 marks $6\frac{1}{2} \times 9\frac{1}{2}$; 86 (paper) *Jena*

This monograph, in the series edited by Professor Goebel, is a contribution to the morphology, embryology and cytology of the liverworts. There is a bibliography of sixty-six titles.

MORPHOLOGY

ANATOMY OF THE WOOD RAT. *Comparative Anatomy of the Subgenera of the American Wood Rat (Genus Neotoma). Monographs of the American Society of Mammalogists. No. 1.*
By A. Brazier Howell.
The Williams & Wilkins Co.
$5.00 6×9; x + 225 *Baltimore*

This is a thorough descriptive treatise covering the external morphology, osteology, myology and visceral anatomy (alimentary tract and urogenital system) of the sub-genera of wild wood rats, *Neotoma*, *Homodontomys* and *Teonema*. Besides being a contribution to comparative mammalian anatomy, it will be found useful by all the hosts of laboratory workers who use the white rat as material. The book is well, though not lavishly, illustrated. The last chapter is devoted to a discussion of muscle action and limb motion—functional anatomy of the muscular system in short. There is a brief bibliography and an index.

CARL GEGENBAUR. *Rede zum Gedächtnis seines hundertsten Geburtsjahres, gehalten im Hörsaal der Anatomischen Anstalt in Heidelberg am 19. April, 1926.*
By Friedrich Maurer. Gustav Fischer
1.20 marks $6\frac{1}{2} \times 9\frac{1}{2}$; 18 (paper) *Jena*

A brief review of the life of the great comparative anatomist, with some portraits.

PHYSIOLOGY

L'EXPLORATION FONCTIONNELLE DU FOIE ET L'INSUFFISANCE HÉPATIQUE.
By Noël Fiessinger and Henry Walter.
Masson et Cie.
$1.20 $6\frac{1}{4} \times 9\frac{1}{4}$; 387 (paper) *Paris*

This book will interest those specialists in internal medicine who are trying today to find some method of estimating the function of the liver. Unfortunately for the authors, our knowledge of the physiology of the liver and of bile pigment formation has grown so rapidly in the last two years, since this book was written, that it can hardly serve as a text for the man who is on the firing line of research. It will, however, be a help to those students who wish to know more about the history and development of the subject, particularly in France. Over a third of the book deals with the clinical picture of hepatic insufficiency and methods of treatment. There is no index.

THE RESPIRATORY FUNCTION OF THE BLOOD. *Part I. Lessons from High Altitudes.*
By Joseph Barcroft. *The Macmillan Co.*
$5.00 $9\frac{1}{4} \times 6\frac{3}{4}$; x + 207 *New York*

The deserved success of Professor Barcroft's *The Respiratory Function of the Blood* has necessitated the preparation of a second edition. The advance in the subject has meanwhile been so great as to make it desirable to split the book into a series of volumes, of which this is the first. It deals with the results of the author's various physiological expeditions to high mountain localities. The book is by way of being a classic.

BEZIEHUNGEN ZWISCHEN CHEMISCHER KONSTITUTION UND PHYSIOLOGISCHER WIRKUNG.
By E. Rost. *Urban und Schwarzenberg*
1.20 marks 7 x 10; 24 (paper) *Berlin*

The correlation between the chemical composition of drugs and their physiological actions constitutes one of the prime problems of pharmacology. The present contribution, which is a reprint from the *Handbuch der praktischen und wissenschaftlichen Pharmazie* edited by Thoms, is a brief review of the present state of knowledge of this field of investigation. There is a fairly extensive bibliography.

BIOCHEMISTRY

SURFACE EQUILIBRIA OF BIOLOGICAL AND ORGANIC COLLOIDS.
By P. Lecomte du Noüy.
Chemical Catalog Co.
$4.50 6 x 9; 212 *New York*

This contribution to the American Chemical Society's Monograph Series is of interest to both biologists and students of molecular physics. It recounts in detail the distinguished author's own researches at the Rockefeller Institute. Starting from the theoretical inferences as to equilibrium which can be made from the Gibbs-Thomson thermodynamic formula Du Noüy demonstrates experimentally "that the proteins and other substances which constitute living matter have a tendency to concentrate at interfaces. They even carry with them part of the salts which, if alone in a solution, would show the opposite tendency. The precipitation or the coagulation of proteins may in certain cases be facilitated by

this accumulation of the molecules. But a still more important conclusion can be drawn: i.e., that the most probable configuration of equilibrium of such a system is the cell form."

ENZYMES. *Properties, Distribution, Methods and Applications.*
By Selman A. Waksman and Wilburt C. Davison. The Williams & Wilkins Co.
$5.50 6 x 9; xii + 364 *Baltimore*

This useful digest of the literature on enzymes is divided into four main parts, which deal successively with the properties of enzymes, their distribution among living organisms, methods of preparing and studying them, and their practical application in the arts and industries. There is a biblography of over thirteen hundred titles, and an index. The book will be a valuable work of reference in every biological laboratory.

LE pH INTÉRIEUR CELLULAIRE.
By Paul Reiss.
Les Presses Universitaires de France
50 cents 10 x 6½; 135 (paper) *Paris*

A detailed critical review of the literature regarding the determination of the hydrogen ion concentration of the contents of the individual cell. It will be a useful work of reference for all cytologists and experimental biologists generally. There is a bibliography covering some seven pages. The author has himself done considerable original work in the field.

PHYSIKALISCHE CHEMIE DER ZELLE UND DER GEWEBE.
By Rudolf Höber. Wilhelm Engelmann
42 marks 6¼ x 9½; xvi + 955 *Leipzig*

The sixth edition of a standard treatise, which has now indeed become a classic in the field. This edition is considerably revised from the fifth, of two years ago, the separation between pure and applied physical chemistry particularly being made more sharp.

HYDROGEN ION CONCENTRATION. *Its Significance in the Biological Sciences and Methods for its Determination. Vol. I. Principles of the Theory.*
By Leonor Michaelis. Translated from the German by Wm. A. Perlzweig.
The Williams & Wilkins Co.
$5.00 9 x 6; xiv + 299 *Baltimore*

It has been necessary in the second edition of Dr. Michaelis' well known treatise to divide it into two volumes. The first, now before us, deals with the fundamental principles of the theory of physical chemistry, while the second will discuss methods of measuring hydrogen ion concentration, and applications. The book has become one of the classic texts of modern biology and medicine.

LEHRBUCH DER PHYSIOLOGISCHEN UND PATHOLOGISCHEN CHEMIE. *In 75 Vorlesungen. Für Studierende, Ärzte, Biologen und Chemiker. I Band: Organchemie. II Lieferung: Muskel- und Nervensubstanz, Stütz- und Gerüstsubstanzen, Leber, Niere und Lymphatische Organe. Vorlesung XVII bis XXIX.*
By Prof. Dr. Otto Fürth. F. C. W. Vogel
15 marks *Leipzig*
10 x 7; v + 207 (paper)

This second part of the second edition of Professor Fürth's textbook of physiological and pathological chemistry maintains the high standard of quality set in the first part, which was reviewed in an

earlier number of The Quarterly Review of Biology.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 202.* Containing following articles: *Flockung von Kolloiden* and *Die Bestimmung des isoelektrischen Punktes*, by Ernst Bloch; *Methoden zur Bestimmung der Adsorption*, by Andor Fodor; *Methoden der biologischen Dispersoidanalyse*, by Friedrich-Vincenz v. Hahn; *Ermittlung der Struktur von kolloiden Mizellen*, by Rassa Riwlin; *Ultrafiltration und Elektro-Ultrafiltration*, by Heinrich Bechhold.

Urban und Schwarzenberg
9.30 marks 7 x 10; 210 (paper) *Berlin*

This part of the Abderhalden handbook concerns itself with various aspects of the physics and chemistry of colloids, a subject just now greatly to the fore in various fields of biology.

SEX

SEX AND THE YOUNG.
By Marie Carmichael Stopes.
G. P. Putnam's Sons
$2.00 $5\frac{1}{4}$ x 8; 248 *New York*

A wide-ranging discussion of the problems presented in the instruction of children in sex matters. Much of the advice given is excellent. The point of view underlying the whole book is the prevalent one that the child ought to be protected, guided, instructed and perhaps even coddled by older persons, instead of being left to develop his or her own knowledge of sex in his or her own way. Perhaps this is true. But it involves a curious point of logic. Of the arguments advanced by Stopes (and many others) for telling children all about sex early and often, *are* true, how does it come about that all, or at the very least nine-tenths, of the generation to which we belong and those to which our fathers and grandfathers belonged, were not physically and morally wrecked for the lack of these biologically proper parental precepts about sex, which we and our forebears wholly missed? It is a great puzzle. Perhaps all these lives *were* ruined and we never knew it.

PROBLEMS OF HUMAN REPRODUCTION.
By Paul Popenoe.
The Williams & Wilkins Co.
$2.50 $7\frac{1}{4}$ x 5; ix + 218 *Baltimore*

Some years ago there was a good deal of talk about the dreadful consequences of the assumed widespread and complete ignorance of the young about sex and reproduction. At the present moment there appears something like one book a week which tells all. Mr. Popenoe has lately been specializing in this field, with a flux of mingled physiology and moral precepts. The present volume seems to us a little better than some other "sex" books, perhaps because it contains more physiology and less preaching.

BIOMETRY

DIE INTRAINDIVIDUELLE FLUKTUIERENDE VARIABILITÄT. *Eine Untersuchung über die Abänderung des Pflanzenindividuums und die Periodizität der Lebenserscheinungen. Botanische Abhandlungen, Heft 9.*
By E. Dennert. *Gustav Fischer*
7 marks $9\frac{3}{4}$ x $6\frac{1}{2}$; 149 (paper) *Jena*

An interesting biometrical study of intra-individual variation of the parts,

mostly leaves, of single plants. It is chiefly valuable for the data it presents. The biometric technique employed is very simple and scarcely adequate to any really penetrating analysis of the problem.

PSYCHOLOGY AND BEHAVIOR

THE INFLUENCE OF NURTURE UPON NATIVE DIFFERENCES.

By Truman Lee Kelley. The Macmillan Co.
$1.40 5 x 7½; vii + 49 *New York*

An ingenious, if perhaps not entirely convincing, attempt to measure separately the effect of inheritance and of learning in the determination of the differences among individuals in respect of certain mental characteristics and abilities. The argument and technique are statistical in character and are stated very obscurely. The sort of final conclusion reached is indicated in the following statement, which however is to be understood as applying only to the abilities mentioned: "We may therefore conclude that approximately 97 per cent of the adult difference between Arithmetic, Reasoning and Spelling abilities is to be attributed to original nature. Thus nurture has in the long run negligibly influenced the native idiosyncrasies in abilities in these two fields."

THE POSSIBILITY OF METAPHYSICS. *A Course of Four Lectures Delivered Before the University of London in March, 1924.*

By Hans Driesch. The Faith Press, Ltd.
2s. 6d. 7½ x 5; 63 *London*

A contribution to theology by the distinguished professor of philosophy at Leipzig, and erstwhile zoologist. He has travelled a long way from sea-urchin eggs. It seems unlikely that biologists will be either thrilled or helped greatly by this treatise. Driesch states categorically (p. 58) that he is convinced that telepathy, mind-reading, clairvoyance, telekinesis, materialization and perhaps also premonition, *are facts*, and that they are more satisfactorily explained by the spiritualistic hypothesis than any other.

L'ART ET LA RELIGION DES HOMMES FOSSILES.

By G. H. Luquet. Masson et Cie.
$1.04 6½ x 10; 231 (paper) *Paris*

The position taken in this extremely well illustrated and printed treatise is the one widely prevailing at the present time, to the effect that the art of the prehistoric cave-dwellers found its basic motivation in religious and magical considerations. This may be true, but the evidence in its favor so far produced by anyone, including M. Luquet, seems to us to fall short of demonstrating this thesis. But objectively the book is fascinatingly interesting.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

SCIENCE OF LOVE WITH KEY TO IMMORTALITY.

By Ida Mingle.
School of Liveable Christianity
$5.00 5¼ x 8¼; 1118 *Chicago*

The title of this book is informative in more senses than one. It will be recalled that the phraseology of this title is extraordinarily suggestive of that of another book, also bound in black cloth. Perhaps still another religion is being born in our midst, and perhaps this book with its

thirty-six lines (numbered) to its eleven hundred odd pages is its epic.

We can advise no one either to buy it or to read it through. But dipping in it yields entertainment. Like most religions it has a lot of sex in it. Indeed there seems to be overtly more of it in this treatise than in any other holy writings we are able at the moment to recall. The author is said to be "conspicuous for her capacity to explain all activities of life without condemnation, thereby becoming a fit instrument to write a book of such stupendous significance."

The book starts off, as it should, with evolution:

> The suggestion that man was once a monkey or some other form of anthropoid makes interesting delusion, but not good sense nor science. Man-like creatures are the result of the mixing of the animal mankind with the he and she monsters of the lower animal kingdom. Records of evolution show that when the Third Root race was forming and what is called man was only a huge animal, not yet directly controlled by the spirit of the Gods, a cross took place between the lower and the higher forms of these animal creatures, thereby crossing in the blood stream the spirit of the man-creature with the spirit of the beast. This cross was a sexual cohabitation and in a later cycle was repeated at the introduction of the white race into the regions of Australia, this cross producing the sterility and ultimate extinction of the Bushmen.

This, we submit, is getting away to a good start. It would be, like Artemus Ward's bear, amusing and instructive, to develop some other of the high spots of the book with quotations. But the QUARTERLY REVIEW OF BIOLOGY is a family magazine, and furthermore its financial position will not warrant the risk of having a number barred from the mails. Were it not for these inhibitory considerations the chapters on Generative Marriage; Material and Spiritual Marriage; Man-Woman; Soul-Mates; Divorcement; The Seed of the Woman; Christ, Jesus Christ, and Jesus; etc., etc., could yield up one of the most curious messes of nonsense that our readers have ever met. Under the circumstances the best we can do is to offer to let anyone who will come to Baltimore read the office copy for one hour without charge. That will be enough.

BLOOD AND SUPERMAN.
By H. Valentine Knaggs.
The C. W. Daniel Co.
3s. 6d. $7\frac{1}{4} \times 4\frac{3}{4}$; 92 *London*

Mr. Knaggs is a prolific writer on various subjects from onions to rheumatism. But this book is perhaps his masterpiece. He says at the start that its subject-matter is "to a large extent based on Theosophical teaching." Unfortunately we cannot spare the space to detail all the wonderful conclusions reached. One sample will have to do. "Blood, by reason of its odorous principles which pass along the nerves, is the source from which our intellect is built up by the mind. There are three factors which build intellect: (1) The free mixing of blood that takes place among the more progressive races of mankind; (2) the stimulating diet—e.g. meat, sugar, alcohol, drug beverages and tobacco—to which Western nations are addicted; and (3) the intense thirst for wealth and enjoyment which is a feature of our modern life. Ancient man was *clairvoyant, but devoid of intellect.*"

REGINALD'S FATHER

Our new office boy, Reginald, comes of good sound New England stock, with traditions of reading and general interest in intellectual matters back of him. Furthermore there is a transparent and vigorous sincerity and honesty in the blood which is as rare as it is appealing

in our over-urbanized and over-sophisticated civilization.

Testimony to these qualities is borne by the following letter, which Reginald's father sent in the other day.

To the Editor,
Dear Friend:

We have seen much in the newspapers lately about evolution. Not knowing much about it I bought and read, after seeing the account of it in the Quarterly Review of Biology last year, a copy of a new and up-to-date book called "The Ways of Life" by Professor Lull of Yale College. I found it pleasant reading, and very informing to a plain farmer like myself, who has had plenty of chance to observe Nature, though but little to read books.

The Professor records many of the wonders of Nature in this book. I was especially struck by the following sentence on p. 65: "In certain of the New Brunswick rivers the capelin run at times in such great numbers as to fill the stream from bank to bank, and in such relic seas as the Caspian, where the number of kinds of animals are few, but of individuals very large, the cessation of fishing for a single day is said to make an appreciable increase in their numbers."

Now I never have myself fished in the Caspian Sea, but a cousin of my wife has a farm on the Lallegosh River in New Brunswick, and has many times seen just such runs as the Professor describes. He tells often of the run of the spring of 1917, when the fish were so packed in the river bed opposite his farm that all the water in the river was forced out and overflowed his cornfield to a depth of three feet. In fact the overflow extended clear to the house, and filled the cellar up to the second step from the top of the cellar stairs. The fish in the river were a sight which attracted all the farmers from the countryside, and a good many from the cities, even as far as St. John. Unable to swim, because they had crowded all of the water out of the river bed, the fish stayed packed solidly together headed upstream for eleven days. Then a sharp shower fell, beginning about half past two in the afternoon. Owing to the fact that the rubbish left by the visitors, who had come to see this curious sight, and picnicked along the shore, had raised the bank for about one foot for a distance of nearly two miles, this shower provided enough water to enable the fish to move on.

I am glad to be able on the unimpeachable testimony of a relative of the family (who is a professing brother of the Adventist faith) to confirm the Professor's account. In a way I can offer direct testimony of my own, because I furnished the seed to replant the cornfield. Furthermore it is nice on our side to have the Professor's confirmation, because some people have refused to believe my wife's cousin when he has told this truly marvelous tale.

It seems to me that some of those fish of the Caspian Sea, of which the Professor tells, ought to be imported into this country. Any fish that will perform in this manner described would be a valuable addition to our resources. The nice adjustment of the females of this species, which leads them to lay eggs all the year round, and in just sufficient numbers to replace the daily catch, is certainly one of the most beautiful adaptations which evolution has produced.

Yours truly,

Nicodemus A. Skillings,
R. F. D. #2
West Brown
Maine.

Reginald adds that the seed corn furnished by his father was a selected strain of Longfellow Flint, which he himself got originally from the Maine Agricultural College at Orono while attending Farmers Week.

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THE QUARTERLY REVIEW of BIOLOGY

ANIMAL BEHAVIOR AND INTERNAL DRIVES

By CURT P. RICHTER
Psychobiological Laboratory, Phipps Psychiatric Clinic, Johns Hopkins University

ONE of the most fundamental of all the phenomena which characterize animal life and distinguish it from plant life is the spontaneous motility of the animal organism. A few plants, to be sure, especially certain forms of marine vegetation, do move about, but these few are exceptions in the plant kingdom. The activity of animals, on the other hand, although it varies widely in form and extent from species to species, is an ordinary phenomenon which one always anticipates under normal circumstances. We may ask, then, what it is that sets off the diverse performances which animals display. Ordinarily we think of most of their activity as being due to some form of external stimulation. We know, however, that all animals, from the lowest uni-cellular organism to man, are active even when all external stimuli have been eliminated. And since this spontaneous motility, just as any other kind of motility, must have a definite cause, it must be due to some natural factor within the organism. Many workers have chosen to call it "voluntary" activity, presumably because of the common belief that the "will" to do is the origin of the action. We believe, however, that spontaneous activity arises from certain underlying physiological origins. We shall attempt to show from studies chiefly on the white rat what some of these origins are, and how they fit into the general biological picture of the animal's life.

The investigations described below have been made by Ging H. Wang, Elaine F. Kinder, Tomi Wada, and the present writer in the Psychobiological Laboratory of the Phipps Psychiatric Clinic during the past six years. Some of the experiments have already been reported elsewhere, but we have taken this opportunity to collect also numerous observations that are as yet unpublished. Of the extensive work on animal "drives" done by Hoskins (1925), Moss (1924), Slonaker (1924, 1925, 1926), Stone (1924, 1925, 1926), Szymanski (1920, 1922), and Tracy (1926) we shall incorporate in this review only that part which bears directly on our own method of approach or on our own experimental findings.

PERIODIC NATURE OF SPONTANEOUS ACTIVITY—TWO-HOUR RHYTHM

We may begin our review with the rat confined just after feeding in a small cage

of the type shown in figure 1. The walls and floor of the cage are absolutely bare and the room in which the experiment is performed is kept constantly illuminated and free from all disquieting noises and odors. If we observe the animal for a while we see that it moves about most of the time, doing many things. It sniffs and claws at the walls of the cage, it climbs, and gnaws and scratches; but from all these observations, however interesting at first sight, we learn nothing of what makes it active. If, however, we arrange the cage so that every movement therein, even the slightest, is recorded over a period of ten to twelve hours on a smoked drum, a remarkable fact comes to light: this diffuse gross bodily activity occurs rhythmically, active periods alternating with periods of almost complete quiescence. The active periods occur at intervals varying from one to two hours. Moreover, the records show further that the activity within each active period is slight at the beginning, but increases as the period advances and reaches its maximum usually near the end (Richter, 1922). Typical records obtained from two rats in triangular cages are shown in figure 2. The record in figure 3, obtained from a guinea pig in the same type of cage, is representative of a similar rhythm found in other animals.

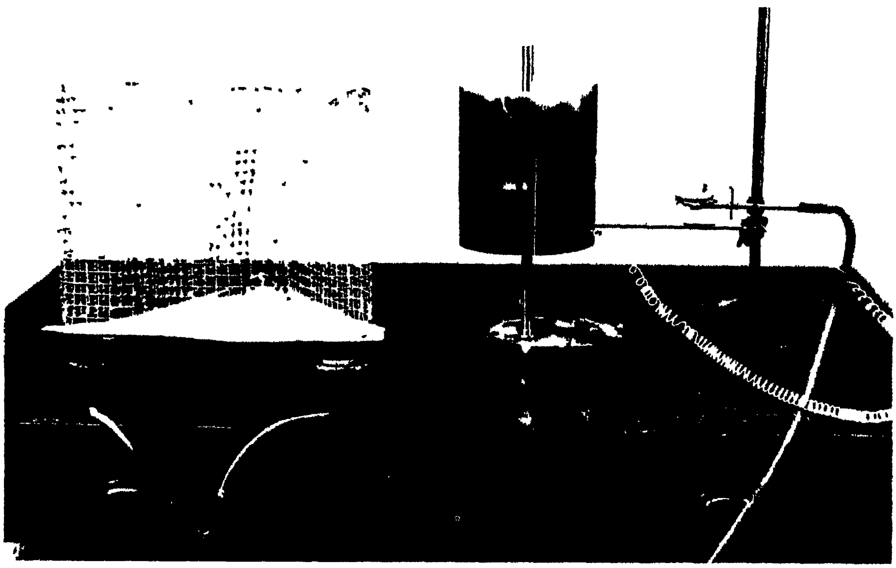


FIG 1 PHOTOGRAPH OF CAGE USED IN STUDYING GROSS BODILY ACTIVITY

The cage is triangular in shape, 12 inches high and 12 inches wide. Each corner is supported on a rubber tambour through which all movements are transmitted to a recording Marey tambour. The time is recorded on the smoked paper in half hour intervals by means of an eight day clock.

Had the motility been irregular and non-periodic we should have accomplished nothing in our investigation of its origin. On the contrary, however, it is very significant that such well defined periods of activity, recurring at such regular intervals, are found when external conditions are as nearly constant as is practically possible. This fact would indicate that the motility rhythm must be set up from within the animal in some organ which functions at a similar frequency of one and a half to two hours.

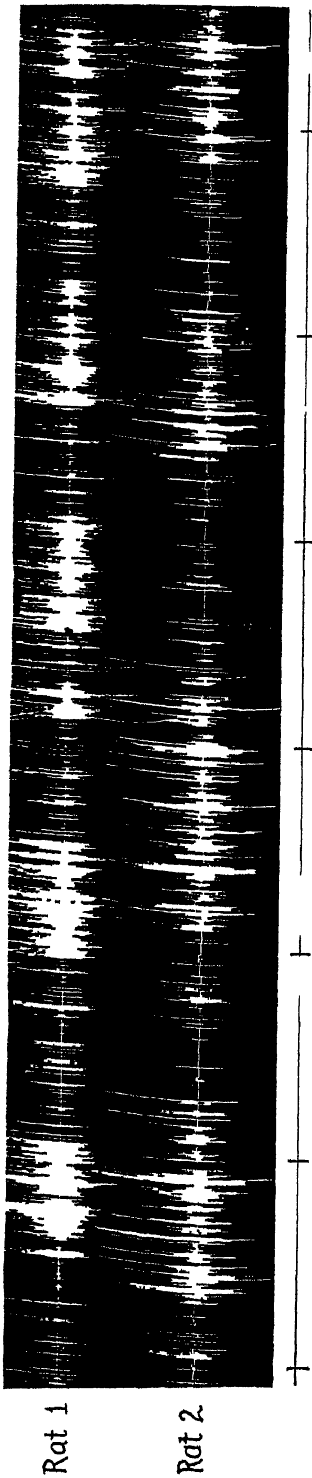


FIG. 2 RECORDS FROM TWO ADULT RATS SHOWING THE PERIODIC NATURE OF THEIR SPONTANEOUS ACTIVITY
Time is given in hours below the record

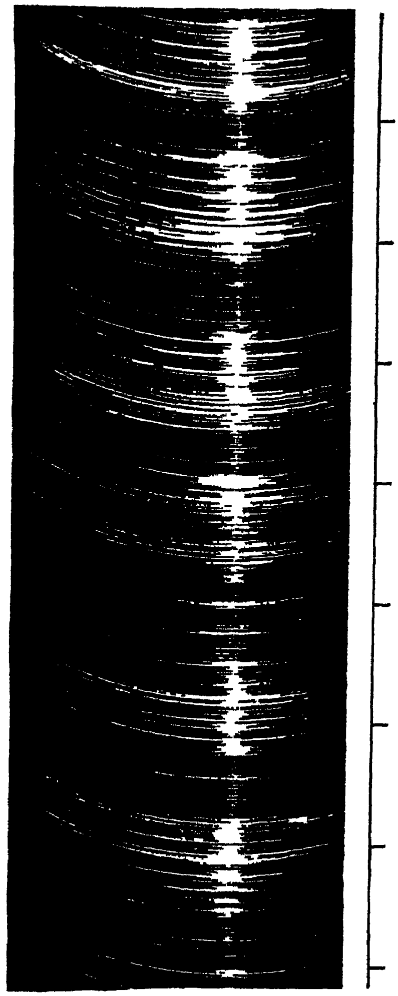


FIG. 3. RECORD OF SPONTANEOUS ACTIVITY OF AN ADULT GUINEA PIG
Time in hours below the record

ORIGIN OF THE TWO-HOUR-ACTIVITY RHYTHM

A review of the periodicity of the different viscera eliminates at once the heart and lungs and the sex glands, since the two former organs function at a frequency much higher and the latter at a frequency much lower than that of the bodily activity rhythm. In the stomach, however, we know that active periods alternate with quiescent intervals every hour and a half to two hours. In 1904 Boldireff was able to show that contractions occur in the walls of the empty stomach, but several years elapsed before entire process is repeated. Thus one period follows another as long as the stomach remains empty.

Gastric movements in both animals and man have been studied by means of the apparatus shown in figure 4 (Martin and Rogers, 1927). A balloon attached to the end of a tube is passed through the oesophagus into the stomach and inflated, and a manometer is fastened to the other end of the tube. The contractions of the stomach change the pressure on the balloon, so that some of the air is pushed up into the tube, and the level of the water in the manometer is changed. As the

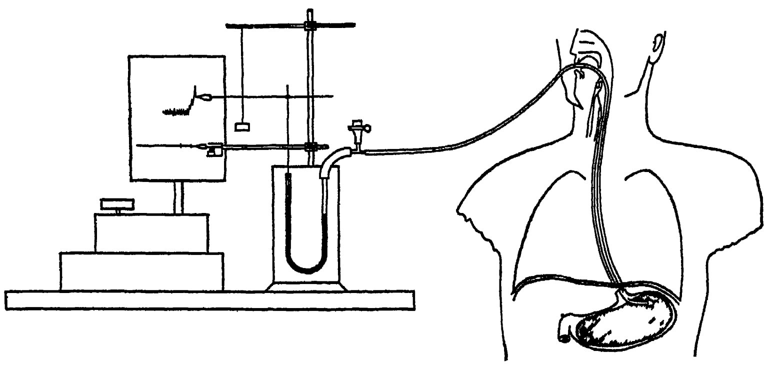


FIG. 4. DIAGRAM SHOWING THE METHOD OF RECORDING THE HUNGER CONTRACTIONS OF THE EMPTY STOMACH (Martin and Rogers, 1927)

Carlson (1916) demonstrated the periodic nature of this activity. Carlson, working with guinea pigs, dogs, and monkeys, found that from one to two hours after a meal, when the stomach is nearly empty, contraction waves begin passing downward over the stomach walls. These waves, small at first, gradually become larger and larger until they finally involve the whole lower half of the organ, and the gastric musculature often passes into a condition of semi-tetanus. Then, quite suddenly, the contractions cease and an inactive interval of an hour or more ensues. After this period of quiescence the small waves begin again, and the water rises and falls with the contraction waves, the movement is recorded by a floating pointer on a smoked drum. A record obtained by this method with similar apparatus is shown in figure 5. The record was taken in this laboratory on a human adult during a night of normal sleep. The portion presented,—that portion registered between 12.30 and 2.30, when the last meal had certainly been assimilated,—illustrates very clearly the cyclic nature of the movements of the empty stomach.

According to the recent observations of Rogers and Martin (1926), the stomach takes the shape shown in figure 6 *A* at

the height of each of the single contractions near the end of the active period and that shown in figure 6 *B* when it is inactive and relaxed. With each of these large waves, then, we see that the lower part of the stomach contracts to such an extent that the lumen practically disappears, whereas the upper part may show a contraction wave near the middle.

Cannon and Washburn (1912) and Cannon (1915) have shown that with these large contractions the sensation of hunger arises, and from the work of Rogers and Martin we know that these "hunger" contractions are set up in the lower third

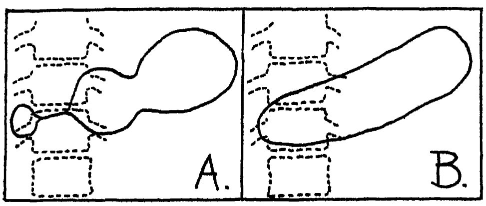


FIG. 6. *A.* SHAPE OF THE STOMACH AT THE HEIGHT OF A CONTRACTION WAVE. *B.* SHAPE OF THE RELAXED STOMACH

(Roentgenographic observations by Rogers and Martin, 1926.)

of the stomach. The hunger sensation is not produced until the end of the active period is nearly reached, when the waves have become very large, but even then it increases in intensity to some extent with the magnitude of the contraction, and it disappears entirely when the contractions cease. The inference, therefore, is quite logical that the two-hour periods of gross bodily activity in the rat are associated with periods of gastric movement and have to do with the hunger responses of the animal.

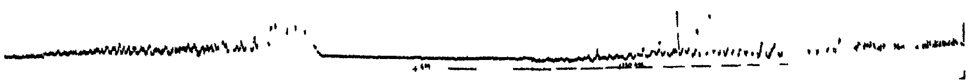


FIG 5 RECORD OF STOMACH CONTRACTIONS OF A HUMAN ADULT TAKEN DURING AN UNINTERRUPTED SLEEP

CORRELATION BETWEEN THE TWO-HOUR ACTIVITY RHYTHM AND THE HUNGER RESPONSE

In order to test this hypothesis we recorded simultaneously the bodily activity of the animal and the intervals at which it sought food and ate. This experiment was performed in the type of cage shown in figure 7. The larger compartment was simply the usual triangular

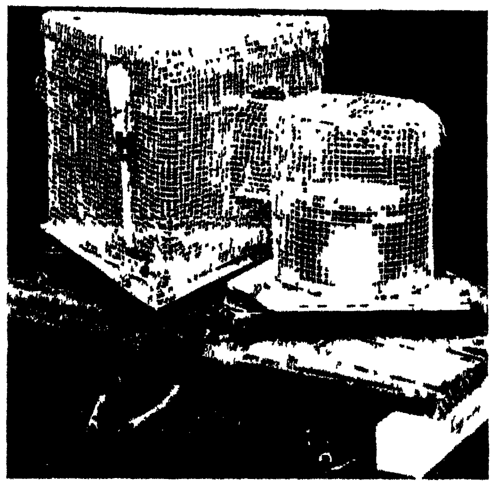


FIG. 7. PHOTOGRAPH OF COMBINED FOOD AND ACTIVITY CAGE

The two compartments are supported on separate sets of tambours so that the activity in each is recorded separately.

activity cage shown in figure 1; the smaller compartment contained a cup filled with a powdered food mixture (McCollum diet). The corners of each cage were supported on rubber tambours and so arranged that the activity in the two cages was recorded separately. In this way the curve in figure 8 was obtained,

where the activity in the large cage is registered on the first line, and that in the food-box on the second, with the time in hours below. It will be seen immediately that the animal always enters the feeding-cage and eats once during each approaches the food-box *except to eat*, and that the vibrations recorded in the activity cage for a short time after it leaves the food-box are produced almost entirely by an extensive cleansing performance which always follows feeding.

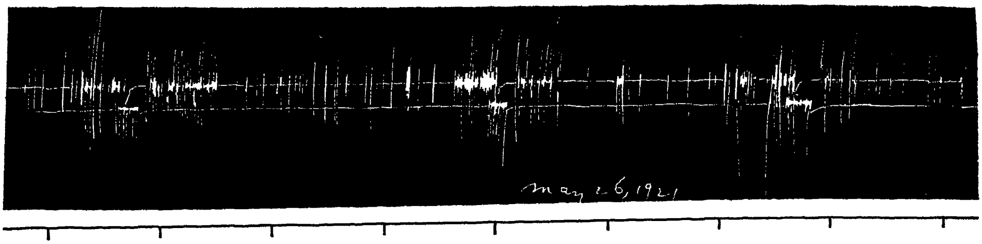


FIG. 8. RECORD SHOWING THE RELATION BETWEEN GROSS BODILY ACTIVITY AND FEEDING PERIODS

Activity in the large cage is given on the upper line, and entrances into the food-box on the lower. Time in hours is indicated below the record.

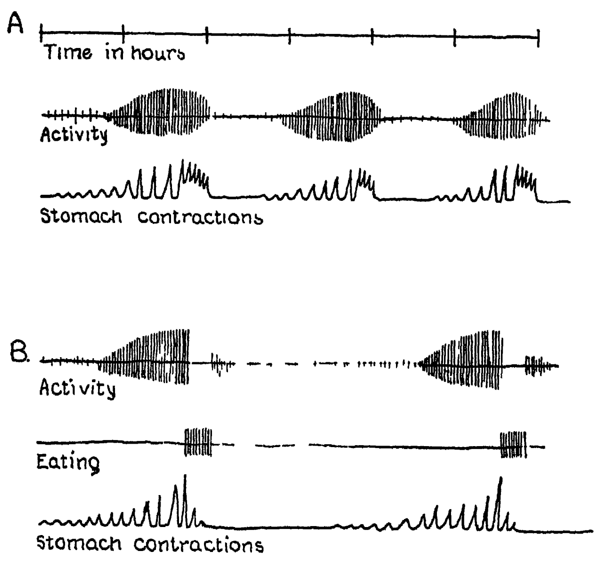


FIG. 9. SCHEMATIC REPRESENTATION OF THE RELATION BETWEEN PERIODS OF GROSS BODILY ACTIVITY AND STOMACH CONTRACTIONS

A. Simple activity cage without food. *B.* Double cage with food

activity period, that it enters usually near the end of the period and rarely at the beginning, and that it does not enter during a quiescent interval. Moreover, we have found through prolonged personal observation, that an adult animal rarely In these experiments the activity periods, recurring invariably with the entrance into the food-box, are even more regular than they were in the earlier work when no food was available. With this greater regularity, the quiescent intervals are

much longer, so that the lapse between periods is three to four hours instead of one to two, as found in the activity cage with no food-box attached. The significance of the lengthened intervals will be discussed below.

We may now attempt to show in more detail how the gross bodily activity, the feeding habits, and the stomach contractions seem to be correlated. The simultaneous records of activity and feeding suggest that a close relationship must exist between the periods observed in the simple activity cage and the hunger "drive" of the animal. From the experimental data compiled above we know that the motility rhythm and the stomach contraction rhythm have three features in common: the frequency of both varies between one and two hours; the active phases of both begin at slight intensity and increase gradually, reaching a maximum near the end; and in both the active period ends abruptly and is followed by a quiescent interval. If we represent the two rhythms as in figure 9 *A*, drawing a diagrammatic activity record directly above a diagrammatic record of gastric movement, so that the active phases of the two coincide, we find that the small stomach contractions occur simultaneously with the beginning of the motility period, and that as the magnitude of the contractions increases the animal becomes more and more active. But how can we justify our representation in terms of the hunger response? It is very probable that as long as the animal experiences the hunger sensation which accompanies the stomach movements, it seeks for food, unsuccessfully, of course, in the single cage without a food-box. When the gastric contractions stop, however, the hunger disappears and the animal becomes quiet again.

On this basis one might expect that when food was available all the time, the rat would enter the food-box as soon as the contractions began. Actually, however, we know that it moves about in the main cage for some time before it approaches the food-box. How, then, can we explain this preliminary diffuse activity? Here again, as in figure 9 *A*, the relationship may be represented schematically. In figure 9 *B*, a record taken simultaneously from the activity cage and the food-box is shown in diagram on the first and second lines, and a stomach contraction record on the third. Thus we see that the small contractions give rise to the diffuse activity in the large cage. The animal seems at first simply to be annoyed and becomes more and more restless as the contractions grow larger, until the "main" contractions set in and the general discomfort becomes centralized in the hunger sensation. This stimulus dominates the behavior of the organism and it enters the food-box to eat. When its appetite has been satisfied, it passes into a period of quiescence which lasts until the stomach has become empty and the contractions have started up again. And since time is required for the contents of the stomach to be digested, the interval between contraction periods is three to four hours instead of one to two hours as observed in the earlier experiments.

We had hoped to establish this relationship in more detail in the rat by means of records taken simultaneously of stomach contractions and gross bodily activity, but all of our attempts to introduce balloons into the stomach of this animal were unsuccessful. It is very difficult to keep it from biting a hole in the tube in the first place. Furthermore, its throat is apparently too small to admit even the finest tube without a severe asphyxia resulting. Because of this failure, we turned our attention to other animals

from which Carlson and his associates had already obtained good records of stomach contractions.

Since the stomach tube can be introduced and fastened very easily in the bullfrog, we experimented on this animal, using the technique of Patterson (1915). The tube and bulb were pushed into the stomach through a small hole made in the skin beneath the throat, and the frog was placed in an activity cage enclosed in a box which could be almost completely darkened. Water from a faucet dripped through on the animal at all times in order to keep it in good condition. In this way

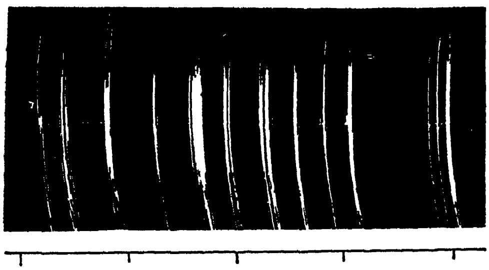


FIG. 10. RECORD SHOWING THE PERIODIC ACTIVITY OF A PIGEON, KEPT IN A LARGE CAGE WITH A PERCH

The bird spent most of its time on the perch, but at quite regular intervals it jumped down to the floor for a few minutes. This record shows the activity on the floor. Time is given in hours below the record.

we obtained stomach contractions which showed no periodicity at all. In one individual, in fact, both the frequency and the amplitude remained constant for eighteen days. The lack of periodicity partly defeated the purpose of the experiment, but not as much as the fact that the frogs remained perfectly still at all times, never making even the slightest movement.

The pigeon seemed more promising for our purposes, since we had previously found its activity to be definitely periodic. The intervals between the periods are somewhat shorter here than they are in the rat, but they are just as regular. The cage used in these experiments was cylindrical in shape, two feet in diameter and three feet high. The circular bottom, made of cardboard, and small enough to fit inside the wire wall without touching it at any point, was supported on tambours so that all movements of the pigeon were recorded on a smoked paper. A wooden rod pushed through the wire wall half-way up, pivoted on a nail at one end and supported on a tambour at the other, served as a perch from which activity could also be recorded. Figure 10, a record of the activity on the bottom of the cage when no food was available, shows that the bird left the perch about once every 20 minutes; and by attaching a recording food-box filled with corn, we found that every time it jumped down it invariably stopped to eat. Rogers (1916) has demonstrated a thirty-minute average rate for the active period of the crop of the pigeon, observing at the same time that it was most restless when its crop was contracting. We attempted, therefore, to record simultaneously the crop contractions and the activity in the larger cage, but the bird always managed to expel the tube no matter how carefully it had been inserted and fixed.

We sought our relationship next in experiments on the human infant. Wada (1922) found that in a child ten months old, during a continuous uninterrupted sleep lasting eight hours, the activity, as recorded by a tambour and spring placed beneath the crib, was definitely periodic, the interval between the periods averaging forty-five minutes. This seemed to offer us an excellent opportunity, especially since Carlson and Ginsburg (1915) had found that the stomach tube could be passed quite easily into infants. Our plan was to take simultaneous records of the stomach contractions and the activity

periods during sleep. In six babies used for these experiments we succeeded in passing the tube without too much difficulty, but then either the babies would not go to sleep, or else the tube was completely blocked by strong spasms of the cardiac sphincter. After many unsuccessful attempts this method of attack had to be abandoned.

Meanwhile, Wada, taking records on medical students while they slept, succeeded in obtaining some very conclusive results. The students swallowed the stomach tube at ten o'clock in the evening, just before retiring, and simultaneous records were taken throughout the night of the stomach contractions and bodily movements. Besides diffuse activities such as turning over, smaller movements were recorded whenever possible. Adult activity during sleep, just as infant activity, proved to be periodic, but the interval between the periods is much longer, varying between two and three

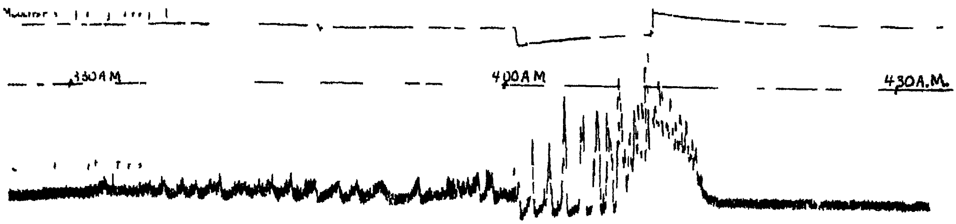


FIG. 11. SIMULTANEOUS RECORD OF GROSS BODILY MOVEMENT AND STOMACH CONTRACTIONS OF A HUMAN ADULT TAKEN DURING DEEP SLEEP

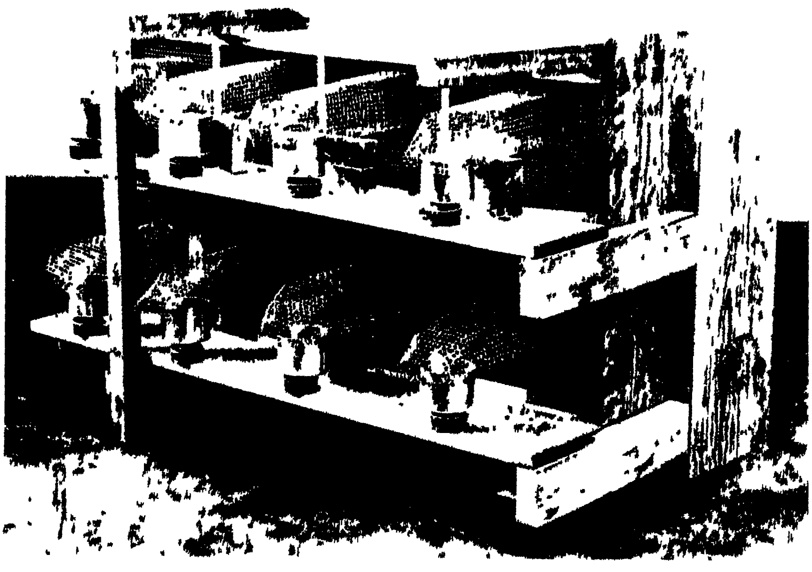


FIG. 12. CAGES USED FOR STUDYING FOOD-HABITS

hours. The stomach contractions, of course, are also rhythmical, much more so than they are during the waking state. And the periods of these two phenomena coincide very well; when the stomach is quiescent the gross bodily activity is reduced to a minimum, but during the contraction periods frequent movements occur, the largest coinciding with the "main" hunger contractions. The record in figure 11 illustrating this fact is similar to those obtained by Wada. The body movements indicated on the top line in this figure were recorded by means of a tambour and spring attached from beneath to the spring of the bed. Since only large movements such as turning over are registered in this way, it can be seen that just before the "main" hunger contractions set in, the subject became very active, and again almost simultaneously with the largest contraction wave there was an even greater amount of activity.

The results of most of our supplementary experiments, therefore, while not conclusive, would seem to uphold our theory that the two-hour activity rhythm in the rat is dependent on gastric function.

FEEDING HABITS OF THE RAT

Starting from our observations on the relation between activity and the feeding periods of the rat, we decided to extend our investigation to a study of its food habits, with special reference to their regularity. For this purpose cages shown in figure 12 were constructed. They consisted of individual compartments large enough for the animals to take plenty of exercise, with a small tunnel on one side at the top leading to the food-box. This tunnel was built in an inconvenient position in order to discourage the rat as much as possible from entering it except when driven by hunger. The food-cup was placed at the end of the tunnel under the wire cloth floor, and a hole was made in the floor just large enough for the rat to insert its head. Whenever it reached in for food, the balance of the cup on a large tambour was disturbed and a mark was made on a smoked drum.

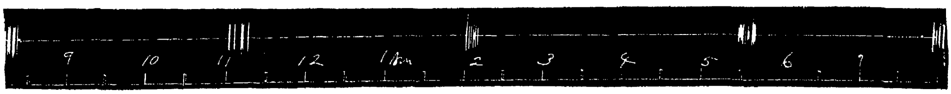


FIG. 13. RECORD SHOWING THE FEEDING PERIODS OF AN ADULT RAT
Time is registered at half-hour intervals

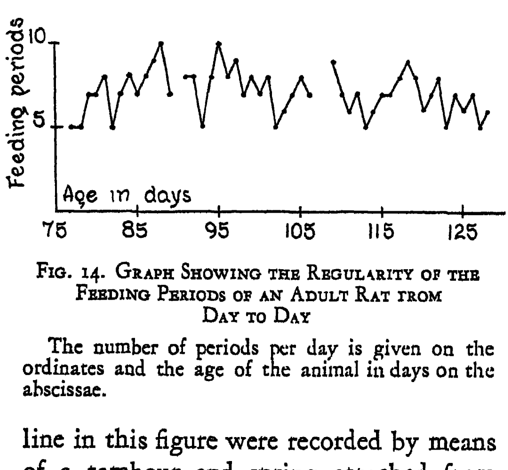


FIG. 14. GRAPH SHOWING THE REGULARITY OF THE FEEDING PERIODS OF AN ADULT RAT FROM DAY TO DAY

The number of periods per day is given on the ordinates and the age of the animal in days on the abscissae.

The records obtained in these cages bring out clearly the great constancy of the feeding habits of the rat. The record in figure 13, taken on an adult animal from 8 p.m. to 8 a.m., shows that the feeding period recurred about once every three hours throughout the day, and when the experiments were extended over a longer time, it was found that the rhythm persisted very constantly from day to day (See fig. 14). Similar experiments on

other animals confirmed these results. A rat may eat seven times a day or it may eat eight or ten times, but in any case it maintains a constant average from one day to the next. The degree of variability of

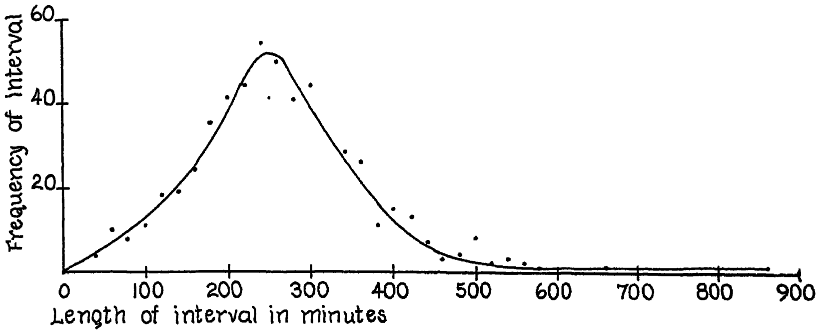


FIG. 15. FREQUENCY CURVE OF INTERVALS OF VARIOUS LENGTHS BETWEEN FEEDING PERIODS IN FOUR ADULT MALE RATS FOR TWENTY DAYS

the feeding response is shown very clearly by the curve in figure 15, compiled from records taken on four animals for twenty successive days. The abscissae represent the length of the intervals recorded between feedings, and the ordinates indicate the number of times each interval was recorded from any one of the four individuals. The curve is evenly balanced with a mode of two hundred and fifty minutes, or approximately four hours. The few longer intervals, we believe, may be identified entirely with periods during which the rat, like the human being, slept in spite of the stomach contractions.

From the above experiments it seems fairly well established, then, that the hunger contractions stimulate the organism to activity, but what the details of the mechanism are we are not prepared to discuss. We do believe, however, that somehow, with each new hunger contraction period, impulses are sent up the afferent nerves from the stomach to the brain and out to the striped muscles, to release the energy stored up there.

GENESIS AND DEVELOPMENT OF THE FEEDING HABITS

But how does the activity produced in this way become associated finally with

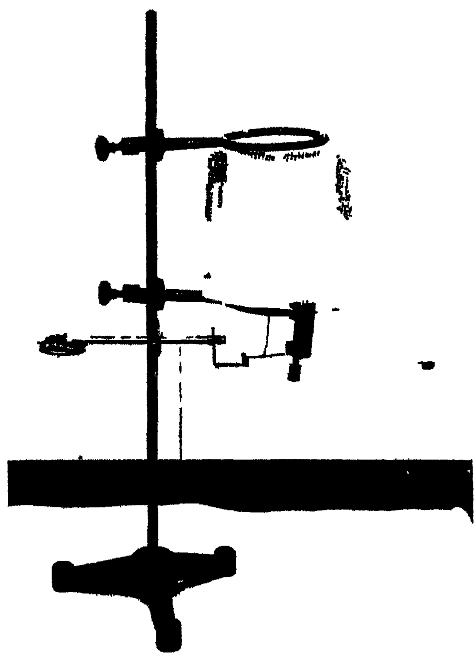


FIG. 16. PHOTOGRAPHS OF CAGES USED IN RECORDING ACTIVITY OF NEW-BORN RATS

the eating process? We cannot assume that the new-born animal seeks food

when the contractions begin. Indeed it would seem more probable that the relationship is built up by the usual trial and error method. In order to solve this problem one must learn more about the activity of the very young animal. Does it show the periodic motility of the adult individual?

The activity of the new-born rat was recorded from the cages shown in figure 16. The bottom of the cage consisted of a wooden frame 6 inches square with a sheet of rubber dam stretched taut across it. The rubber was covered with pieces of flannel and the sides of the cage, made of paper, were pasted on the wooden frame. Every movement of the animal in the cage was transmitted through the rubber membrane to a lever which recorded on a smoked paper drum. The young rats were left in the cages for twelve hours at a time, and then returned to their mothers for twelve hours.

Records obtained in this way showed that the motility of the rat immediately after birth is continuous rather than periodic (See fig. 17). For the first ten days it remains constant; then a rhythm begins to appear, and by the sixteenth day clear-cut and very regular intervals are present. This result is consistent with the fact that the new-born of some anima species show stomach contractions with almost no indication of periodicity (Patterson, 1914). On the basis of this knowledge, then, we may picture how the diffuse activity of the new-born rat resolves itself into a search for food.

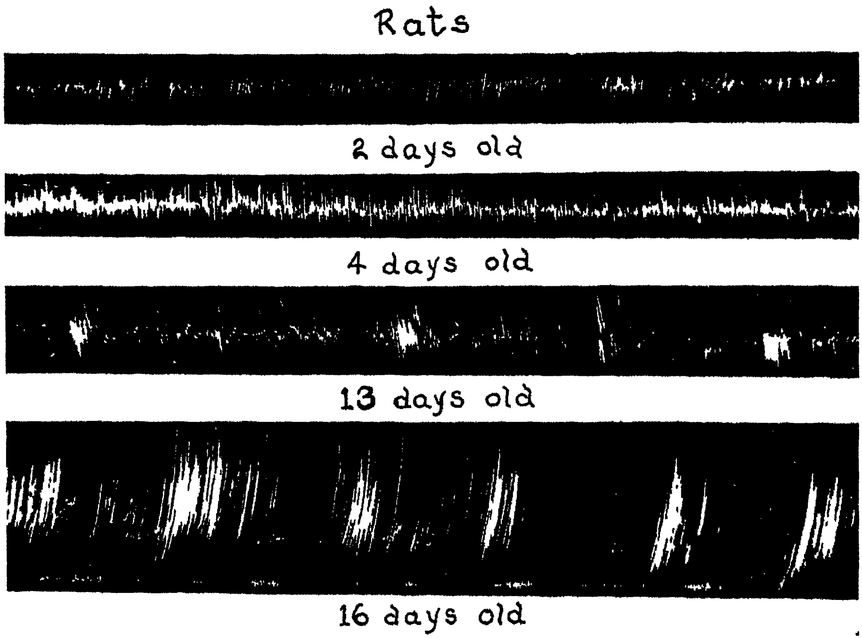


FIG. 17. RECORD OF THE ACTIVITY OF A NEW-BORN RAT TWO, FOUR, THIRTEEN, AND SIXTEEN DAYS AFTER BIRTH

Up to the tenth day the activity is continuous, then it gradually breaks into periods, which, by the seventeenth day, stand out very clearly in the records.

In its almost continuous motility, the very young animal sucks at everything with which its mouth comes into contact,—the feet and legs of its litter

mates, the straw of the nest, hair on its mother's body, and, eventually, the mother's teats. When it sucks at anything other than the teats, nothing results; the stomach contractions persist and the activity continues as before. When it sucks at the teats, on the other hand, an entirely different situation arises; milk teats through the intervention of the mother, but largely by the trial and error method there is gradually established, on a conditioned reflex basis, an association between discomfort due to stomach contractions, feeding, and subsequent relief. In the adult rat, the preliminary restlessness which occurs during the time of small

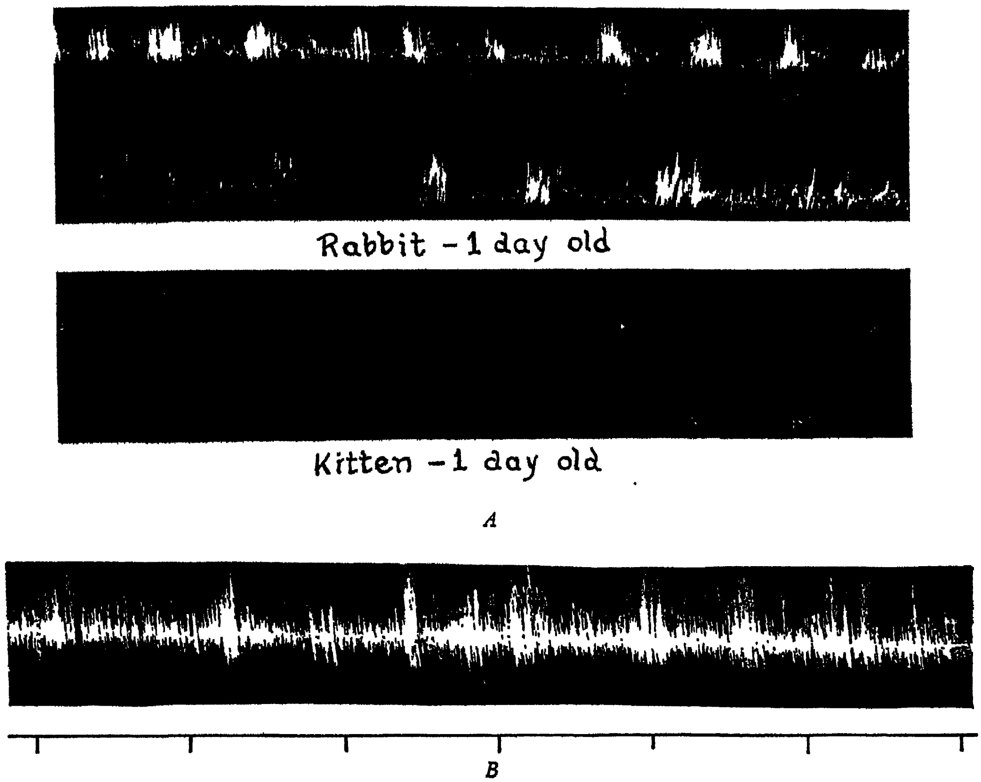


FIG. 18. ACTIVITY RECORDS OF NEW-BORN ANIMALS
A, rabbit and kitten. *B*, chicken. Time in hours below the record

fills the stomach, the contractions cease, and the animal grows quiet. Then as the stomach becomes empty again, the process will be repeated. The animal may happen upon the teats at the very beginning, or it may reach them after a prolonged active interval. In either event, the excursion always ends with the feeding process. The young doubtless frequently find the contractions is diverted at once into specific food seeking activities as soon as the main contractions begin.

It is interesting in this connection that the new-born guinea pig, rabbit, kitten, and chick, unlike the rat, show periodic activity at birth (See fig. 18 *A* and *B*). But how may this fact be brought into relation with the view developed above?

It is important to note that while the rat is still in a comparatively embryonic condition at birth, these other animals are all fairly well developed and coordinated. The rat, for several days after birth, progresses much as a worm does, crawling and wriggling its way about; the new-born guinea pig, on the other hand, actually walks almost at once. In keeping with their periodic bodily activity, the more highly developed individuals probably show periodic stomach contractions at birth. We have as yet done no experiments to test this theory, but we hope soon to observe in detail the feeding habits of these animals to determine how the habits differ from those of the rat with regard to their genesis and development.

FURTHER OBSERVATIONS ON THE PERIODIC NATURE OF SPONTANEOUS ACTIVITY FOUR-DAY ACTIVITY RHYTHM IN THE FEMALE

So much for the three to four-hour activity rhythm apparent in records taken during twelve to twenty-four hour periods. Our observations must now be extended over days and weeks instead of hours. The small triangular cages are impractical for this purpose because of the length of time required to count the individual marks on the smoked drum record. Activity for long periods can be measured more simply and much more accurately in the type of cage shown in figure 19, which consists of a small living

FIG. 19. APPARATUS USED FOR MEASURING SPONTANEOUS RUNNING ACTIVITY

The living compartment with the food cup and water bottle and the cyclometer and lever, can be seen on one side of the partition, and the revolving drum on the other side. (Richter and Wang, 1926.)

compartment just large enough to accommodate a food-cup and an adult animal, and a revolving drum to which the animal has free access at all times. By means of a cyclometer connected with the axle of the drum by an excentric lever, all revolutions, clockwise and counter clockwise, are recorded. A detailed description of the complete apparatus and method employed is given elsewhere (Richter and Wang, 1926, Richter, 1926, Wang, 1927).

The rat, like many other small rodents, seems to enjoy running and spends much of its time in the drum. Although the daily activity averages between five and ten miles for most of the animals, as many as twenty-seven miles have been recorded for one individual in twenty-four hours.

Here again, casual observation of the running activity discloses nothing of its origin. Continuous records over long periods of time, however, reveal a fact far more striking than the tri-hourly rhythm described above. In the female rat the activity falls into a regular four-day cycle, most females running eight to ten miles every fourth day and but a fraction of a mile on the three days intervening. In the record in figure 20, in which activity measured in the number of revolutions is indicated on the ordinates, and the days of the experiment on the abscissae, the regular four-day peak is very evident. Since this rhythm, which was described independently by Wang (1923) and Slonaker (1924), occurs in an environment free from any cyclic disturbance, it, too, must have its origin within the organism. But what organ functions in the rat at a four-day rhythm?

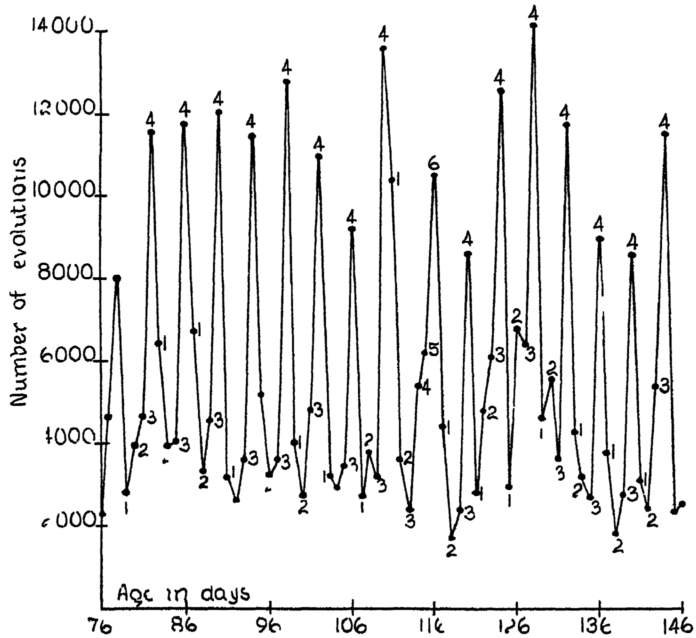


Fig. 20. Running Record of a Normal Female Showing the Four-day Cycle

FOUR-DAY ACTIVITY RHYTHM AND THE OVULATION CYCLE

Observations of the ovulation cycle of the rat made by Long and Evans (1922) answer this question at once. These

workers have shown, by the methods of Stockard and Papanicolaou (1917), that the length of the oestrous cycle in the rat is four days, with individual variations above and below this average. As is well-known, this was determined by histological studies of cast-off cells scraped with a small spatula from the vaginal mucosa. During the dioestrum nucleated epithelial cells and leucocytes are present, whereas during the periods of oestrus and ovulation only cornified cells appear.

Wang and Slonaker have been able to show by means of simultaneous smear and activity records, that the peak of running activity every fourth day just precedes ovulation. This is undoubtedly one of the most interesting correlations that have been made in animal behavior.

The question arises then, as to the relation between the running activity and the sex "drive" of the animal. Wang has found that females will mate for a short time just before and just after the peak of running activity is reached, while at all other times they are completely indifferent or even averse to the male. The exact relationship between running activity, vaginal smears, and sex activity, as worked out by Wang, is shown in figure 21. Records taken every six hours on all three phenomena showed that the great burst in running activity recorded on the day of oestrus is confined almost entirely to the six-hour interval which immediately precedes the appearance of cornified cells in the vaginal smear.

Obviously, therefore, the spontaneous activity is dependent on ovarian function. The degree of dependence can be demonstrated directly by numerous experiments performed on animals in which the ovaries

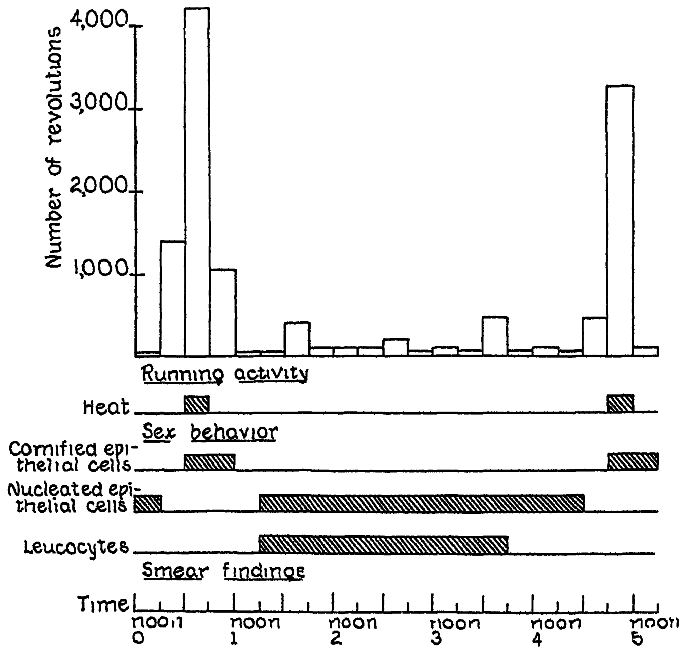


FIG. 21. EXACT TEMPORAL RELATIONSHIP BETWEEN RUNNING ACTIVITY AND THE OVULATION CYCLE, ESTABLISHED BY MEANS OF SIX HOUR RECORDS

(After Wang, 1923)

were not functioning. Pre-pubescence, senility, pregnancy, pseudo-pregnancy, lactation, and castration all show a clear-cut effect in the activity readings. In figure 22, a typical normal record is presented to show the low running level before puberty and the sudden pubescent burst.

Pregnancy causes a 60 to 95 per cent decrease in activity which lasts through the entire gestation and lactation period (Slonaker, 1925; Wang, 1923. See fig. 23). Pseudo-pregnancy, produced when the tip of the uterus is stimulated with a glass rod introduced through the vagina, results in an immediate decrease which persists for fifteen days (Wang, 1923. See fig. 24), and sterile copulation performed by a vasectomized male has the same effect (Slonaker, 1925).

Similar results were obtained in a series of experiments in which a normal female had constant access to a cage containing a vasectomized male. In these experiments a sex-box attached to the usual living-cage connected with the revolving drum, was so arranged that the female could pass freely back and forth to visit the male, but the male could not get into the living cage and revolving drum. This separation was achieved quite simply by means

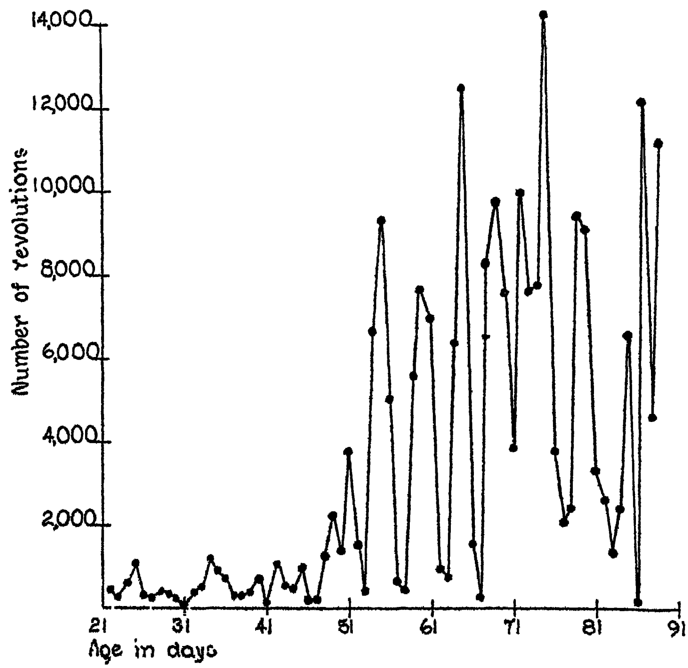


FIG. 22. RECORD SHOWING THE BURST OF ACTIVITY AND APPEARANCE OF THE FOUR-DAY CYCLE AT THE TIME OF PUBERTY

(After Wang)

of a board partition with a hole just large enough to admit the female, but too small for the male. A typical record obtained in this way is shown in figure 25. In order that we might differentiate running activity changes caused by the extra compartment from those caused by the presence of the male, we attached the sex-box a week before the male was introduced. The record shows that the mere addition of the sex cage produced no

effect. When the male was placed in it, however, there was an immediate and prolonged decrease in activity which persisted for eight to ten days after he was removed again.

Figure 26 shows the effect of complete removal of the ovaries: the activity drops (60 to 95 per cent) to a flat, low level and the four-day cycle disappears completely. When an animal is spayed before puberty its activity always remains low and non-rhythmical (Wang, 1923; Slonaker, 1924).

Finally the dependence of the running activity on the ovaries may be demonstrated most strikingly by the effects of ovarian implantation in spayed animals. Whenever the grafts "take," the activity begins to increase almost immediately, and it grows gradually higher until the normal running level of the female is reached. Then, if the grafted ovary is removed, the activity drops about 60 to 95 per cent, just as it does in the normal female after spaying.

These experiments show definitely that the high running level is dependent upon some substance secreted by the ovaries into the blood stream. The question now

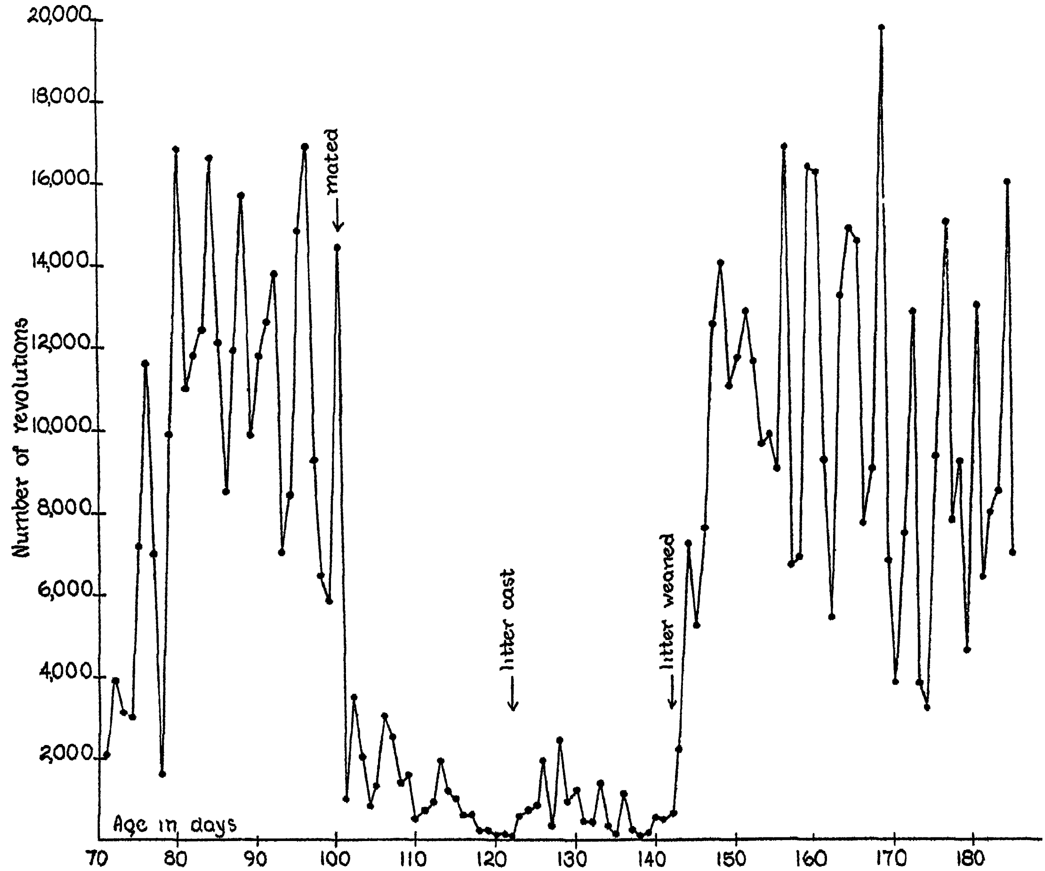


Fig. 23. Record Showing the Effect of Pregnancy and Lactation on Spontaneous Activity

The four-day cycle is absent during pregnancy and lactation, appearing again a short time after the litter is weaned. (After Wang.)

arises as to what part of the ovaries produces this substance. Bugbee and Simond (1926) have thrown some light on this problem by experiments in which the extract from pigs' follicles was injected into spayed rats. Such a procedure produces the same effect that successful implantation of an ovary would have produced,—the activity shows a marked increase from the low spayed level to the level of normal animals and the genital tract resumes its normal condition.

Wang also has obtained these results by the injection of follicular extracts (Unpublished results. See fig. 27). He found that the smear changes are usually detected several days before the activity changes become well defined, and in many instances the activity and smear changes occur independently of each other. Ac-

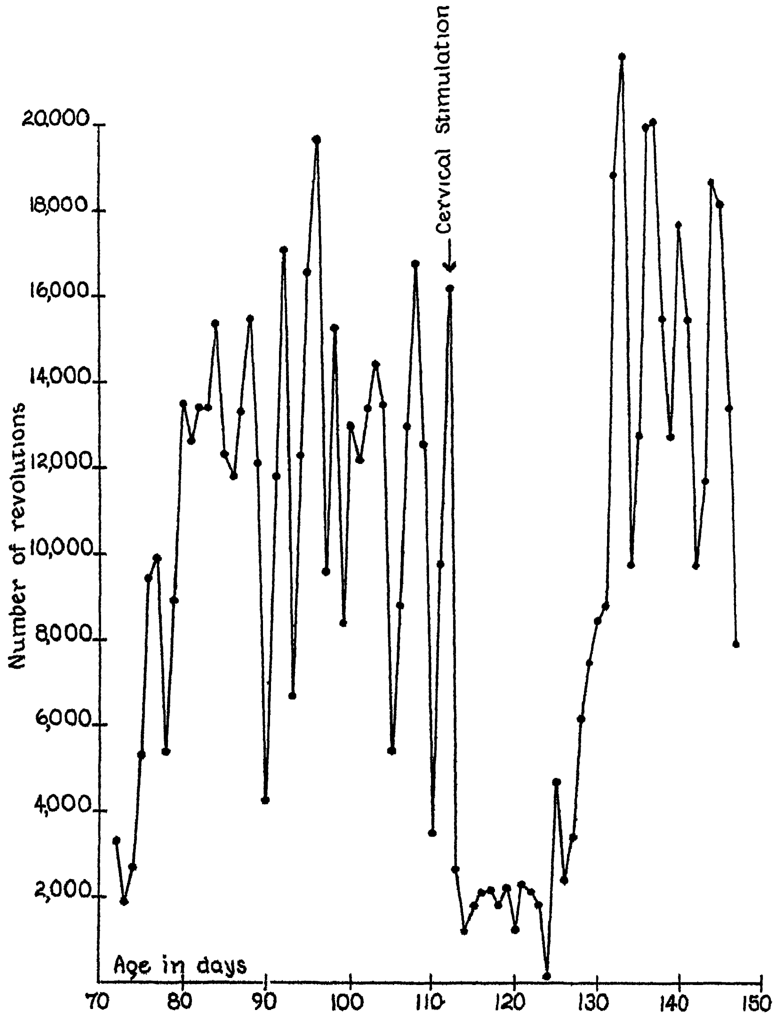


Fig. 24. Effect of Pseudo-pregnancy on Activity
(After Wang)

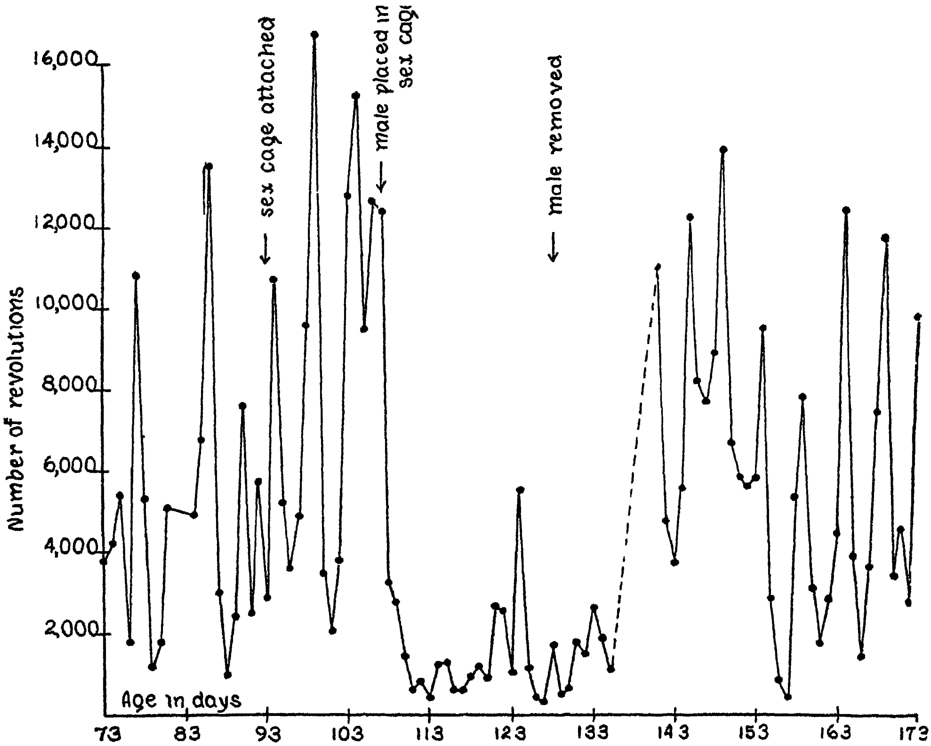
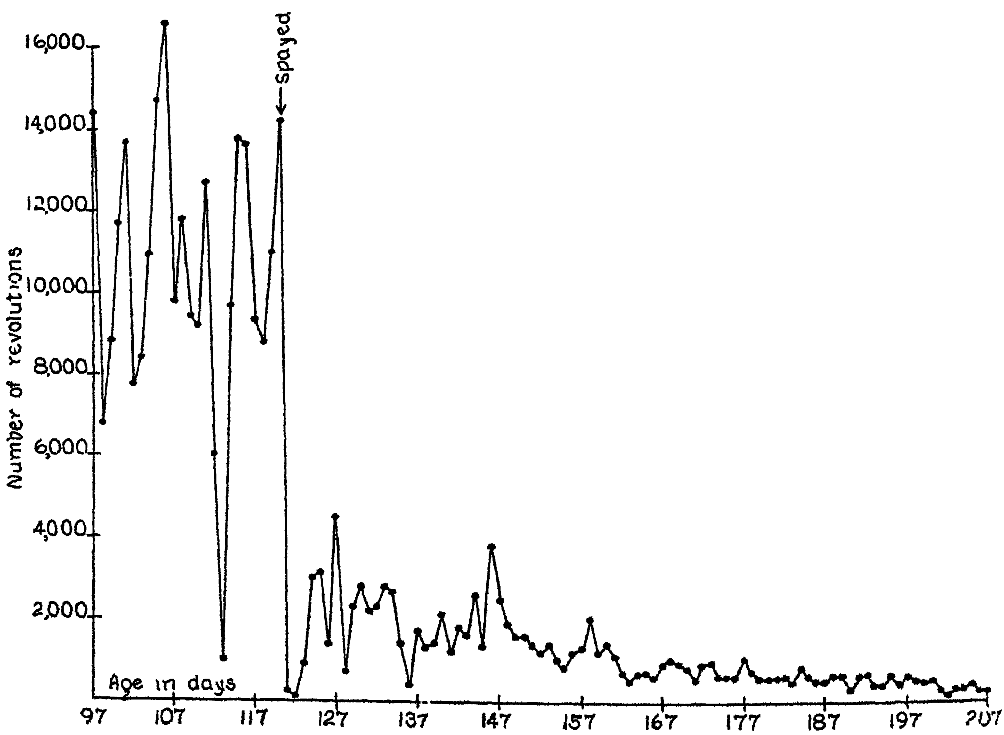


FIG. 25. RECORD SHOWING HOW THE PRESENCE OF A MALE AFFECTS THE ACTIVITY OF THE FEMALE



cordingly he has concluded that there may be in the ovarian secretion one specific substance for furthering the growth and development of the genital tract and another for the production of activity. And on the basis of experiments in which he traumatized the ovaries (Wang and Guttmacher, 1927), this suggestion becomes even more plausible. It was found quite by chance that a small remnant of ovary left in the body produces very striking changes in both smear and activity findings. The activity, except for a drop of short duration immediately following the operation, usually regains its original level, but the four-day cycle is entirely absent. Coincident with the high irrhythmic activity level, the vaginal smears usually show cornified cells, the indication of oestrum in the normal animal. In some individuals, however, the other types of cells, as well as cornified cells, appear and disappear with very little relation to the changes in activity.

The question as to how and where the secretion acts to produce the activity has not yet been answered. We thought at first that, just as the three to four-hour rhythm was set up by stomach contractions, so the four-day cycle might have its origin in the contraction of some similar hollow viscus in the sex-apparatus, probably the uterus. Contrary to our expectations, however, Wang found that removal of the uterus affects neither the level of activity nor the four-day cycle (fig. 28), and Hoskins (1925, II) has recently confirmed these observations. The secretion, then, must take effect in some part of the central nervous system, either by simply increasing the irritability of the centers in the brain and spinal cord, or by actually stimulating those centers. Although definite evidence is lacking at present, we

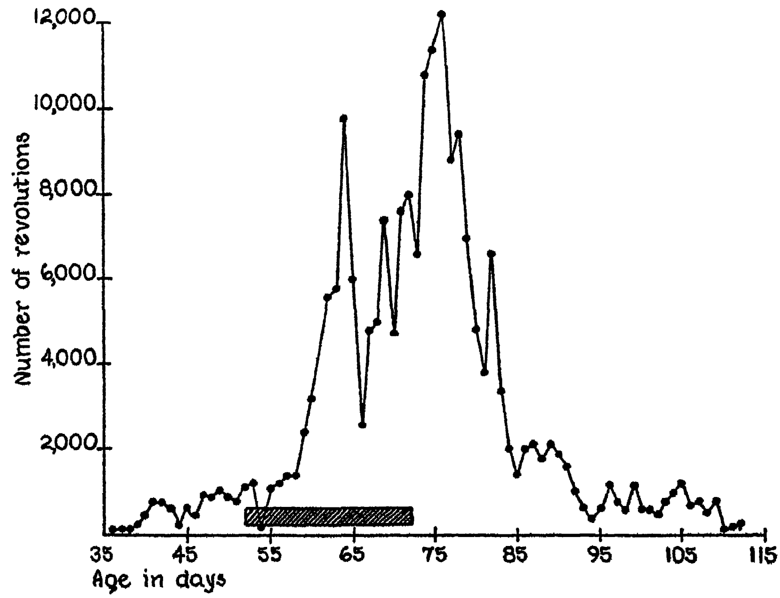


FIG. 27. RECORD SHOWING THE EFFECT OF DAILY INJECTIONS OF FOLLICIN ON THE RUNNING ACTIVITY OF A SPAYED FEMALE

The shaded area indicates the period over which the extract was administered

are inclined to hold to the latter possibility.

SPONTANEOUS RUNNING ACTIVITY OF THE MALE

In the male the spontaneous running activity does not show the four-day cycle of the female, and the general average is somewhat lower. However, it is dependent on the sex glands, for when the animal is castrated the activity drops about 60 per cent to the low level of the spayed female (fig. 29). Hoskins (1925, IV) was able to demonstrate no change in activity when testes were transplanted to the castrate, but we have found that the activity immediately increases to the normal running level (Richter and Wislocki, 1927). And transplantation of ovaries brings about an even greater increase (Wang, Richter, and Guttmacher, 1925). The activity then reaches the high level of the female, and, what is more interesting, it also shows the four-day rhythm (See fig. 30). When the grafts are removed the castrate effects appear again.

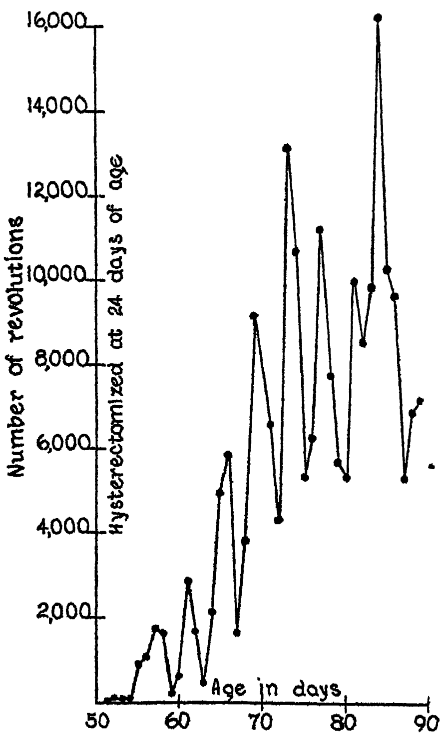


FIG. 28. RECORD SHOWING THAT REMOVAL OF THE UTERUS AFFECTS NEITHER THE LEVEL OF THE RUNNING ACTIVITY NOR THE APPEARANCE OF THE CYCLE

That the relation of running activity to the sex "drive" is not so clear-cut in the male as it is in the female, is demonstrated in a series of experiments in which each male was removed from the running cage for a half hour each day and placed with a female in "heat" in a large stock cage. We found in this way that males showing a low running activity took no interest in the females and made no effort to copulate, whereas males with a high running activity copulated frequently. Contrary to the effect on the females, however, copulation, even when repeated as many as thirty times, produced no noticeable change in the running level of the male on the following day. An activity curve of one of these animals, typical of the entire group, is presented in figure 31.

Nothing is known regarding the mechanism involved in the production of the activity of the male. That the removal of the seminal vesicles produced a no more noticeable effect than did the removal of the uterus in the female is shown in figure 32. We are trying to discover on what part of the testes the activity is dependent by a method similar to that used by Stockard and Papanicolaou in the female. We have been extirpating the testes in some animals at a peak of activity and in others at a depression with the expectation that detailed histological studies of these organs may disclose what parts are responsible for the fluctua-

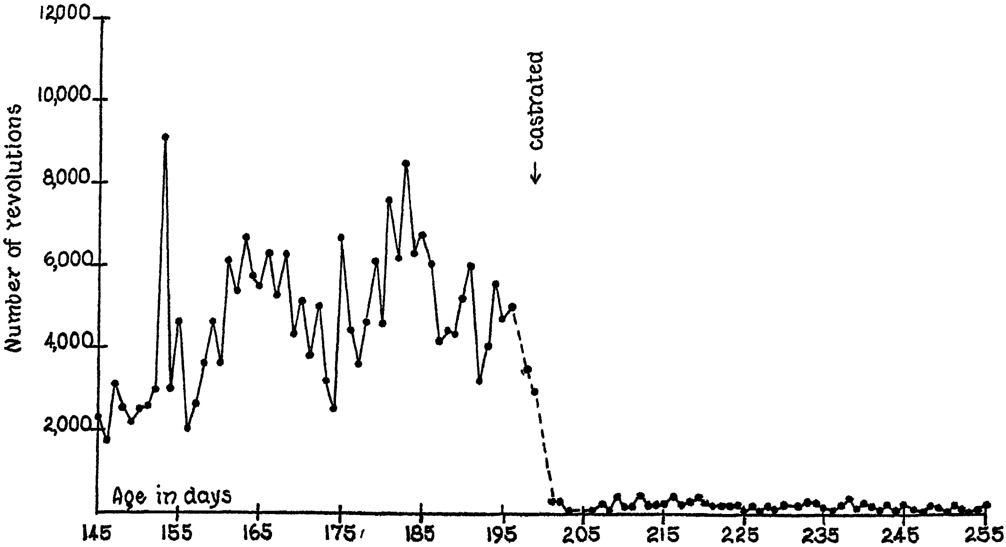


FIG. 29. SPONTANEOUS RUNNING ACTIVITY OF A MALE, SHOWING THE EFFECT OF CASTRATION

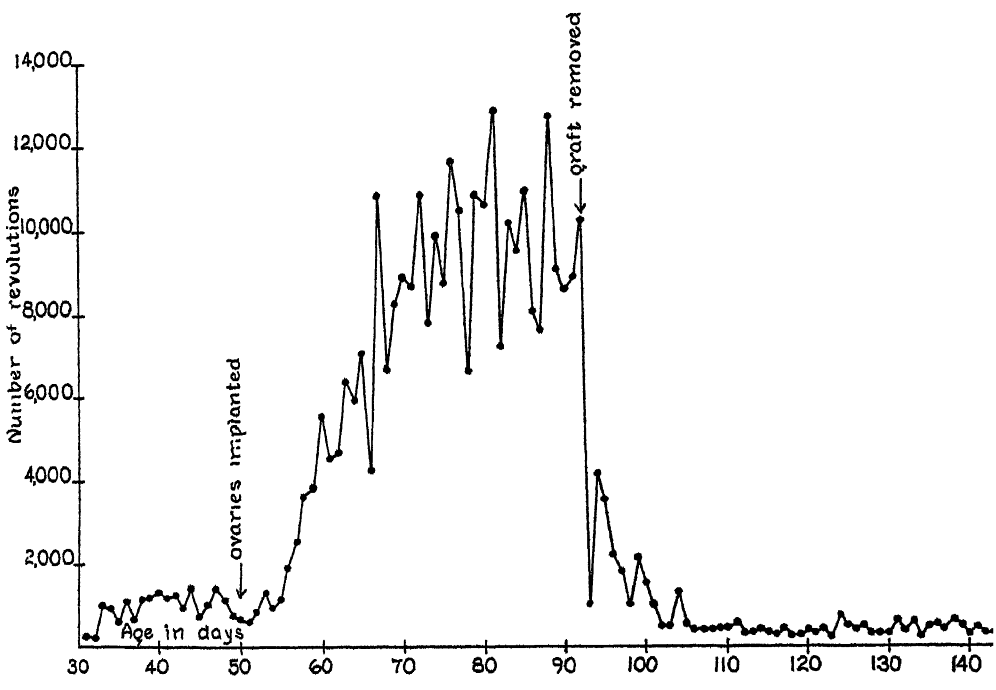


FIG. 30. RECORD SHOWING THE EFFECT OF IMPLANTATION OF OVARIES INTO A CASTRATED MALE

tions in activity. Although we have obtained no conclusive data the approach is promising.

It must be borne in mind before we pass on to a discussion of other rhythms that the work reported above has simply

demonstrated to what extent the overt bodily activity *is dependent* on the sex hormone. None of our experiments has shown that the hormone actually *produces* the activity. Very probably a number of other organs are equally important, so that the elimination of any one of them would be sufficient to bring about the large decrease in activity which follows spaying or castration. We have tried removing the thyroid, hyperthyroid, and the pituitary, but in so far as our operations were successful, they produced no change in activity. Removal of the adrenals, on the other hand, causes a decrease in the running average, although the sex cycle still remains (See fig. 33). It can be seen, then, that we still do not have complete knowledge of the mechanism which determines the composite picture of the spontaneous activity.

OTHER ACTIVITY RHYTHMS

With a knowledge of the cyclic fluctuations in activity we may learn a great deal about changes which occur in the different organs within the body, when outwardly or without sacrifice of many animals nothing could be learned. The discovery of the four-day activity rhythm in the female rat, for instance, would have led very quickly to the discovery of the oestrous rhythm had it not been already detected by other means. This same principle may be applied in a search for cyclic changes in other internal organs, since we have found periods of activity longer than four days in both males and females after the sex organs have been removed. There are at least two other fairly well-defined rhythms, one of from seven to ten days (fig. 34), and one of

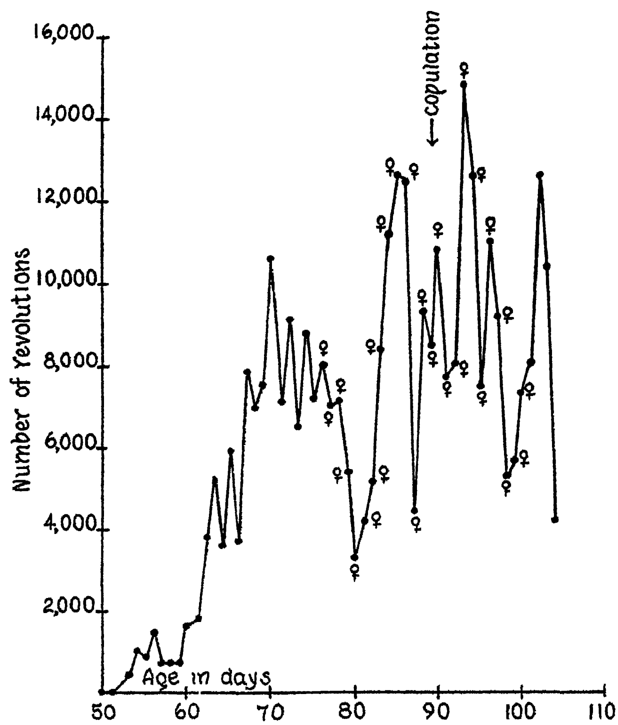


FIG. 31. EFFECT OF COPULATION ON THE RUNNING ACTIVITY OF A MALE

from sixteen to thirty days (figs. 35 and 36). Besides these two rhythms a number of others varying between forty and one hundred and twenty days have occasionally been observed by Slonaker (1926) and by us. Figure 37 shows the activity record of one animal in which a small remnant of one ovary remained.

The question arises now as to the origin and significance of these rhythms. The other internal glands, the thyroid, the parathyroid, the pituitary and the adrenals, suggest a possible source. We have been removing each of these organs at various phases of activity but we have been unable as yet to make a study of the histological sections.

So much for the origin of these rhythms. What is their significance? Are they associated with some specific performance just as the three to four-hour and the four-day cycles are? It may be that, coinciding with these slower fluctuations of running activity, changes in such pursuits as burrowing, climbing, gnawing, fighting, nest-building, and other specific activities can be demonstrated. However, before we take up the question of these more complicated behavior patterns, we must consider briefly some of the purely physiological mechanisms in order that we may comprehend the complete activity picture presented by the organism.

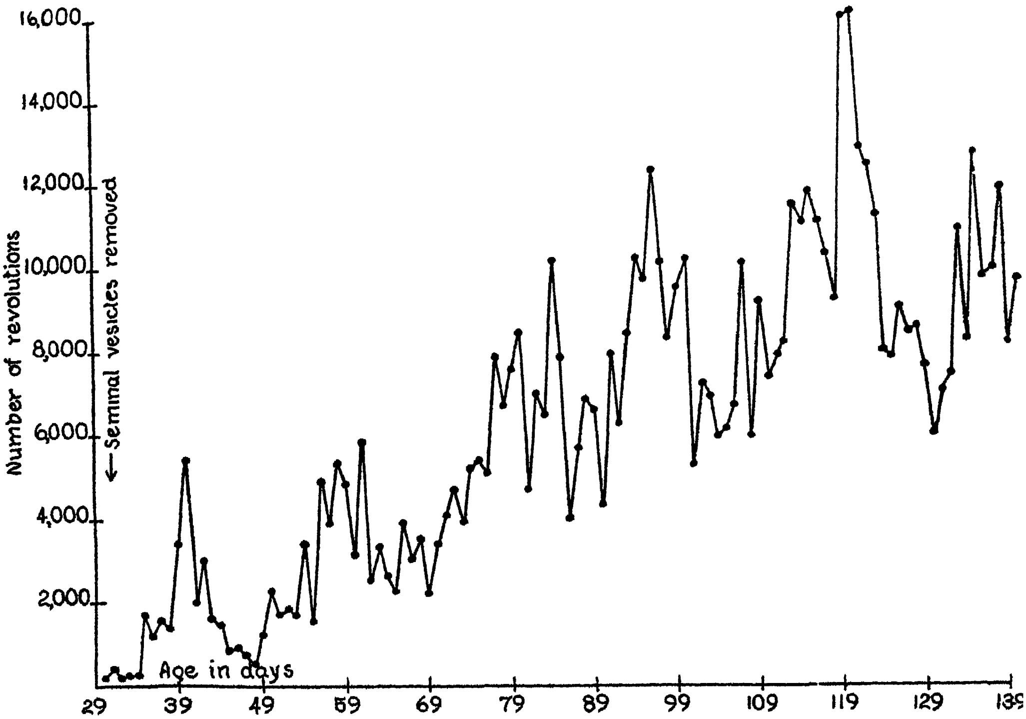


FIG. 32. RECORD OF THE RUNNING ACTIVITY OF A MALE, SHOWING THE EFFECT OF REMOVAL OF BOTH SEMINAL VESICLES

The record differs in no way, so far as we have been able to determine, from that of a normal animal

OVERT RESPONSES OF A PURELY PHYSIOLOGICAL NATURE

For this reason we have studied drinking, urination, and defecation, to deter-

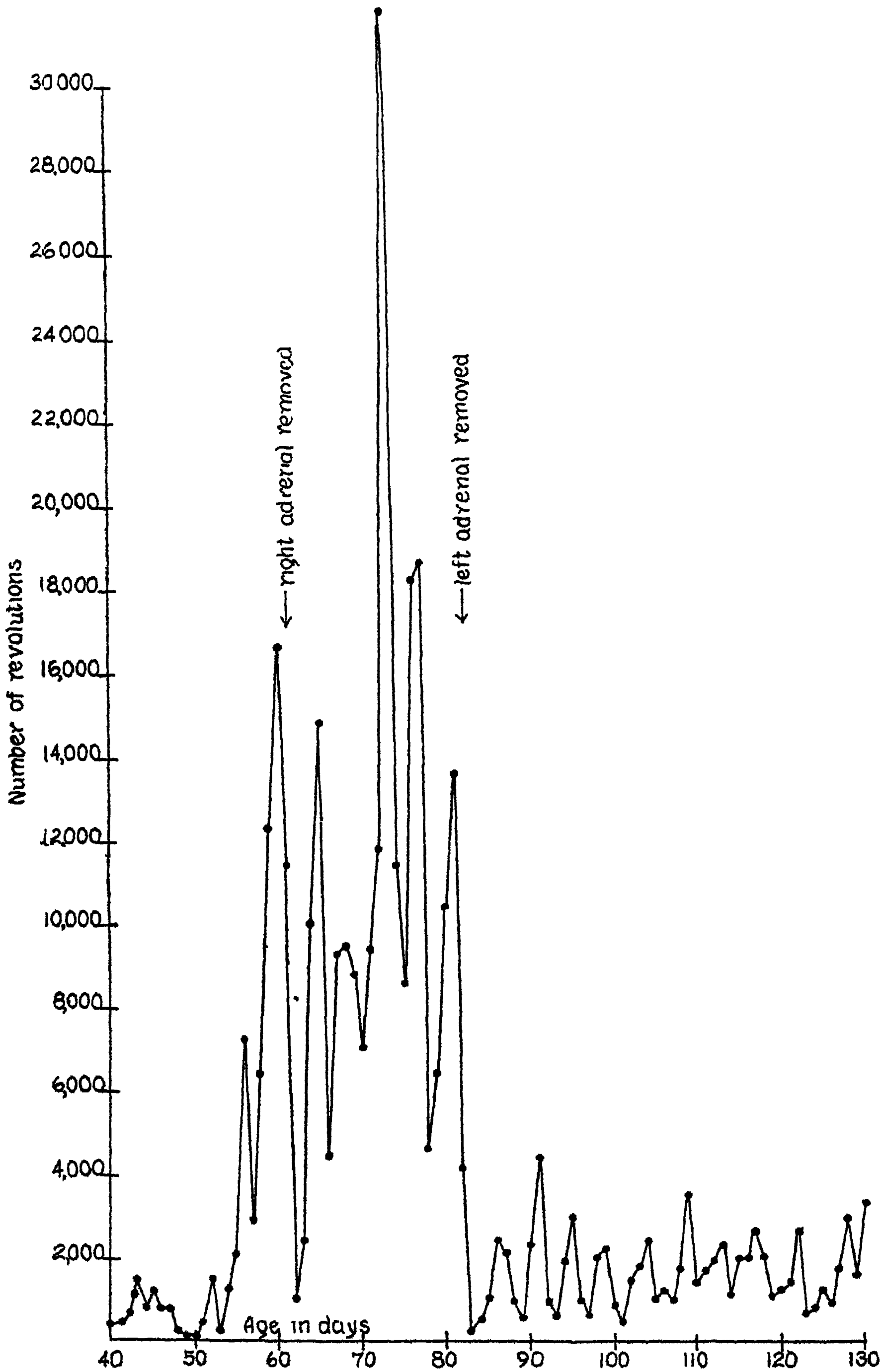


FIG. 33. RECORD SHOWING THE EFFECT OF THE REMOVAL OF BOTH ADRENALS

mine whether these functions, too, are periodic. Records of the time interval at which these three responses occur show that they are all rhythmical.

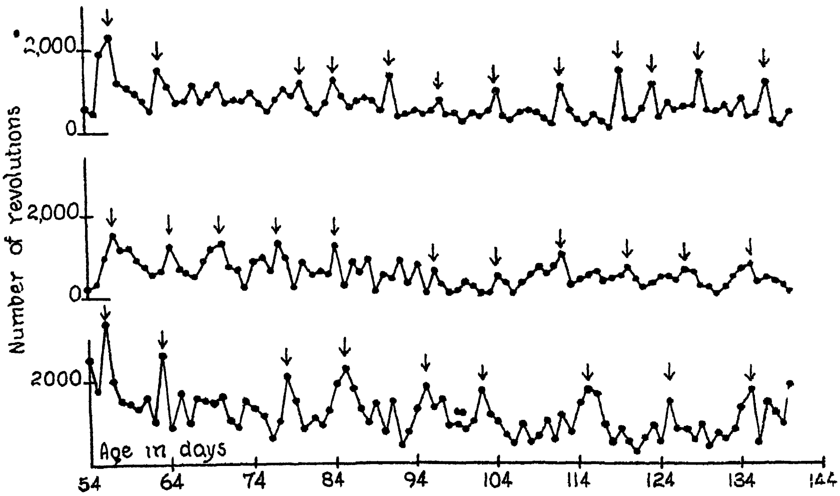


FIG. 34. [R]ECORDS FROM TWO CASTRATED MALES AND ONE SPAYED FEMALE, WHICH SHOW RHYTHMS VARYING FROM 5 TO 8 DAYS

These rhythms have been observed in normals, but they are found most often in castrated or spayed animals probably because of the much lower running activity level.

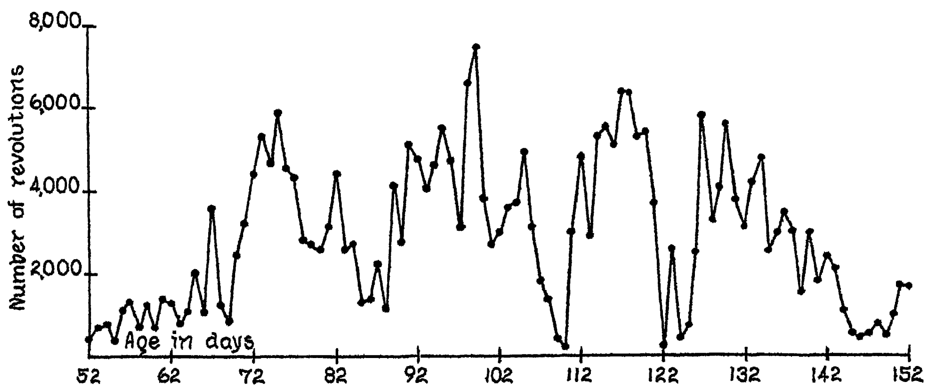


FIG. 35. RECORD OF A NORMAL MALE SHOWING A 16 TO 20 DAY CYCLIC CHANGE IN THE RUNNING ACTIVITY LEVEL

The cycles are much more irregular than the four-day cycle, but they are clearly present nevertheless.

and an inverted watering tube was placed at the end away from the cage. The bottom of this recess was made of a piece of aluminum pivoted at one end and sup-

Thirst was studied by means of the cages shown in figure 38. A recess large enough for the animal to enter and drink, but too small for it to lie down or turn around, was built on one side of the cage ported on a tambour at the other, so that whenever the animal entered to drink a mark was recorded on a smoked drum. The records, as may be seen in figure 39, show that the rat drinks about ten times

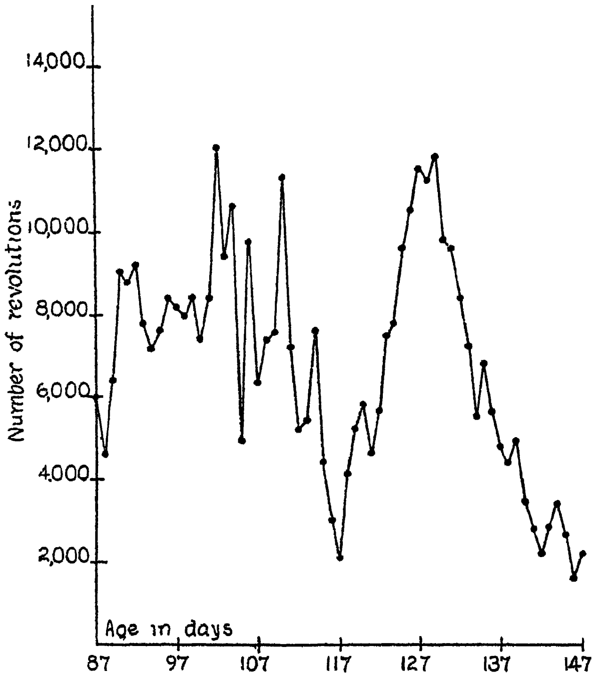


Fig. 36. Record Obtained from a Normal Male Showing One Very Striking Cycle of Twenty-nine Days Duration

The activity mounts steadily for twelve days, then decreases again equally steadily for the next seventeen days. Such regular cycles often appear in the midst of an otherwise very irregular record.

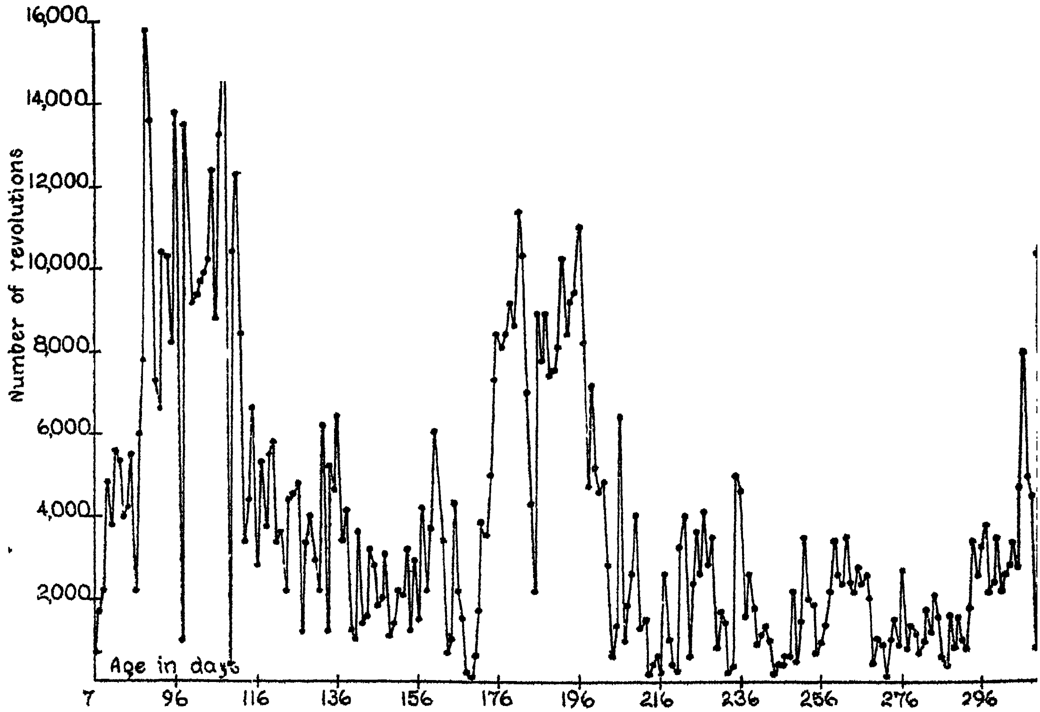


Fig. 37. Graph Showing Cycles of Much Larger Duration,—90 to 120 Days

a day at intervals of two and a quarter hours. The periodicity of the thirst response is quite as remarkable as that of the hunger response, in view of the current conception that the rats eat and drink at very frequent and irregular intervals.

Urination and defecation were recorded in the apparatus illustrated in figure 40. The small cage with a ½-inch mesh wire-cloth bottom, rested over an 8-inch paraffined tin funnel. When the rat defecated, the feces slipped through the wire floor into the funnel and on to an inclined trough of fine-meshed wire below. As they dropped from the end of this trough they struck a small paper disc fastened to

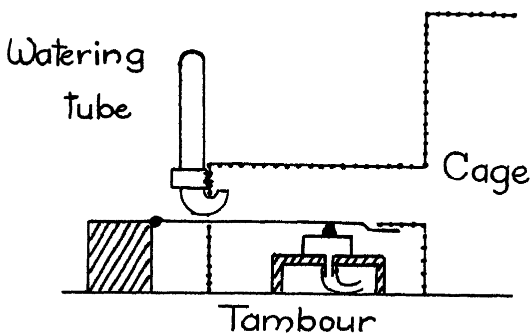


FIG. 38. DIAGRAM OF THE CAGE USED IN RECORDING THE THIRST RHYTHM

the end of a tambour, and the process was recorded as in figure 41. Urine was also collected in the funnel but it passed directly through the wire trough to another paper disc attached to another tambour. A record of urination is shown in figure 42.

From simultaneous records of urination and defecation obtained by this method, it was found that although these two functions are very regular, they are quite independent. Urination occurs approximately every two hours; defecation, every five hours, but the group of animals studied up to the present time is not sufficiently large to permit accurate statements of the time interval, nor can we show how these rhythms vary with age and sex.

These phenomena must reveal the periodicity of the bladder and rectum, but so far we do not know in what organ thirst is localized. Possibly through our knowledge of its periodicity we may obtain some clue as to its origin.

The results of all of the experiments discussed above have shown how largely the spontaneous activities of the rat are periodic in nature, and are associated with periodically functioning organs. From these results, we see the animal as an organism carrying within itself various mechanisms discharging at different rates, to a great extent independently of one another. By way of summary we have listed in Table I the different activities according to their periodicity and the organ with which they are associated.

TABLE I

ACTIVITY	PERIODICITY	ASSOCIATED ORGAN
Urination	2–3 hour	Bladder
Drinking	2–3 hour	?
Defecation	3–5 hour	Rectum
Eating	3–4 hour	Stomach
Mating ♀	4 day	Ovaries
Nest-building	?	?
Gnawing	?	?
Burrowing	?	?
Fighting	?	?
Migrating	?	?
?	7 days	?
?	18–22 days	?
?	40–120 days	?
?	?	Adrenal
?	?	Pituitary
?	?	Thyroid
?	?	Parathyroid

CONSTRUCTIVE ACTIVITIES

With this work on the simpler forms of spontaneous behavior as a basis, we may now single out for study the more

complicated and specific performances of the rat, such as burrowing, gnawing, nest-building, and social activities. At the present time nest-building is the only quantitatively studied. We may ask, then, what it is that makes the rat build nests. In order to answer this question we must arrange our experiment so that

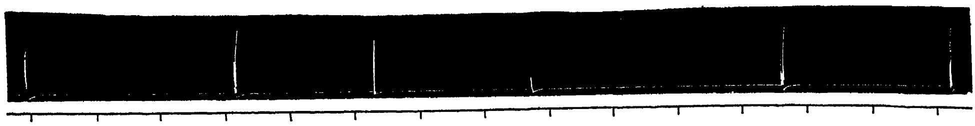


FIG. 39 RECORD SHOWING THE THIRST RHYTHM OF AN ADULT ANIMAL
Time in hours below

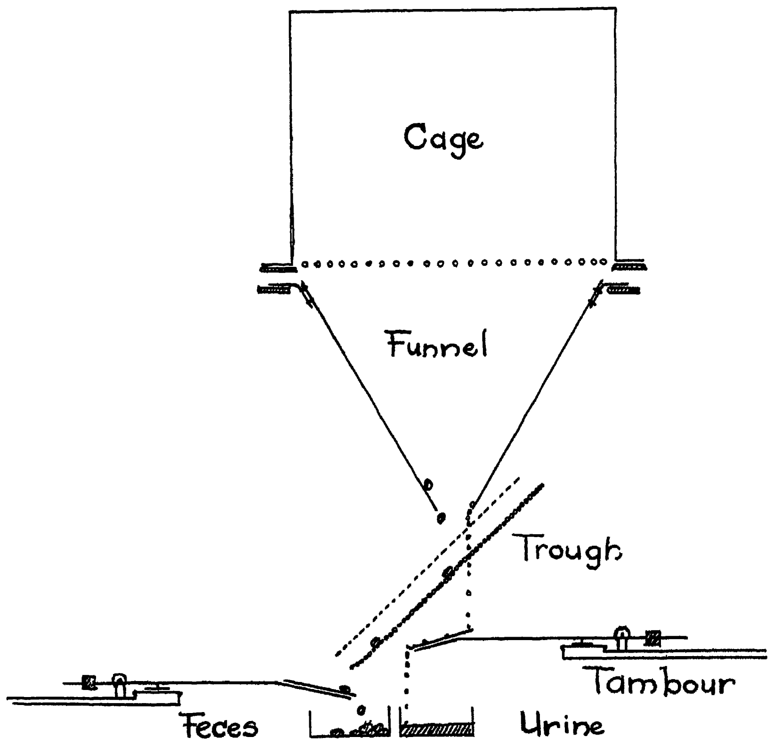


FIG. 40. DIAGRAM OF THE APPARATUS USED IN RECORDING URINATION AND DEFECATION RHYTHMS

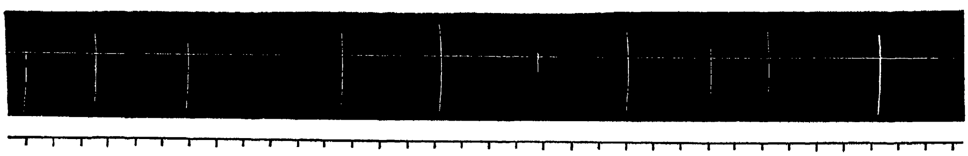


FIG. 41. RECORD OF THE DEFECATION RHYTHM OF AN ADULT RAT
Time in hours below

for the animal, and all other activities are either kept constant or eliminated. Such a situation in which spontaneous nest-building can be measured has been vals tell us nothing about the mechanism involved. Observed over long periods of time under controlled conditions, will it also be periodic like the running ac-

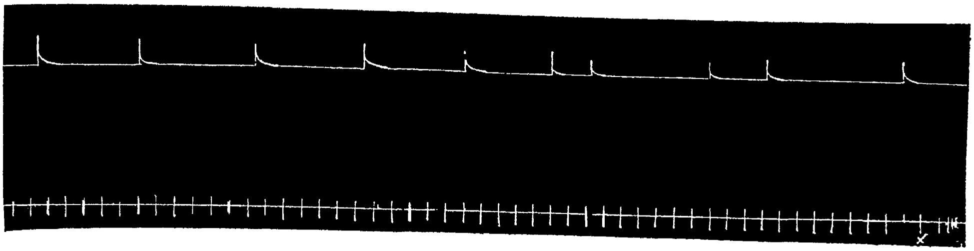


Fig. 42. Record Showing the Urination Rhythm of an Adult Rat
Time in half-hour intervals

worked out very satisfactorily by Kinder (1927), in two different types of cages.

In these cages the activity is measured in terms of the number of strips of crêpe paper used each day by the rat in building its nest. The method of presenting the paper differed in the two types of cages. In the first type 600 strips, ½ inch wide and 6 inches long, were scattered each day evenly over the floor, and the animals built their nests by pushing the strips into heaps. In cages of the second type, (fig. 43 *A* and *B*) 250 strips, 12 inches long, were hung over the sides so that the animal had to pull down one strip at a time and take it to the nest. With these cages Kinder found that if the nests are removed each day rats of all ages will build a fresh nest within the following twenty-four hours. That the activity is present and equally strong in both sexes is shown by the records of the daily nest-building activity of a male and female given in figure 44 *A* and *B*. Moreover, nest-building is practically independent of experience, since young rats thirty days old raised in sawdust build perfect nests out of the crêpe paper the first time it is presented to them. But what is it that drives the rat to build nests? Again observations for short inter-

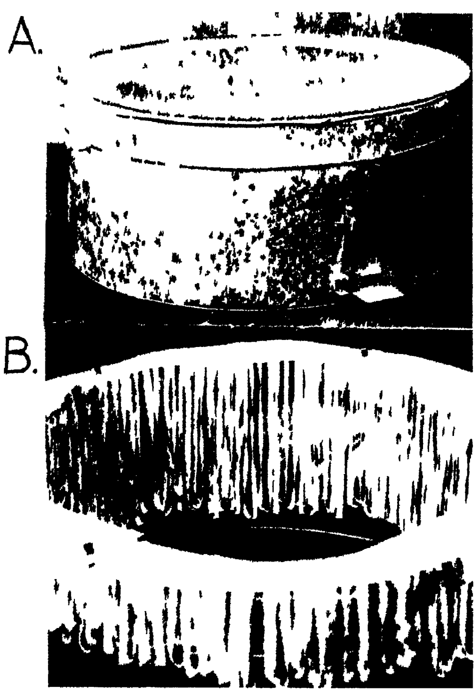


Fig. 43. Photograph of One Type of Cage Used in Measuring Nest-building Activity

A shows the cage assembled without nest-building material. The walls are of galvanized iron and the top of wire cloth. The diameter of the cage is 36 inches and the height 18 inches.

B shows the arrangement of the strips of crêpe paper over the sides of the cage. The strips were hung so that the rats could reach them comfortably only by standing on their hind feet. (After Kinder, 1927.)

tivity? Here Kinder found that the four-day rhythm of the female is present just as it was in the running activity (fig. 45), but it has a very different relation to the cycle. Nest-building is greatest in the dioestrous interval of low running activity and lowest during oestrus when the running activity is highest. At parturition and during lactation the nests are very large, but the controlling mechanism is obviously not an essential part of the reproductive activity since the males often built nests as large as those of the mother rats.

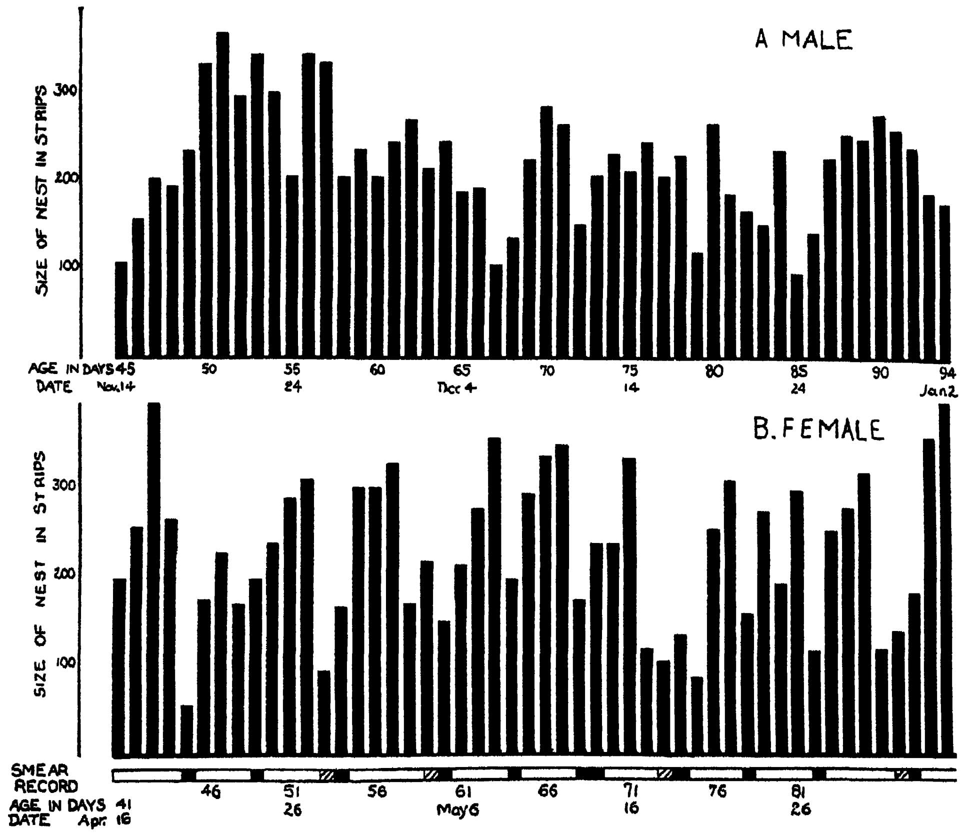


FIG. 44. DAILY RECORDS OF THE NEST-BUILDING ACTIVITY OF *A*, A MALE, AND *B*, A FEMALE, OVER A PERIOD OF 50 DAYS

Kinder found that all phases of the nest-building phenomenon have one feature in common that indicates the origin of the activity: every phase can be understood as a part of the heat-regulating mechanism by means of which the body-temperature is maintained at a constant level. The activity increases in low temperatures and decreases in high temperatures. It is high when there is a tendency for the body temperature to decrease, before puberty, during the inactive dioestrous interval, during pregnancy and lactation, and during starvation; it is low at oestrus, when the animal is very active and the body temperature tends to increase.

We may regard nest-building as a part of the heat-regulating mechanism, just as

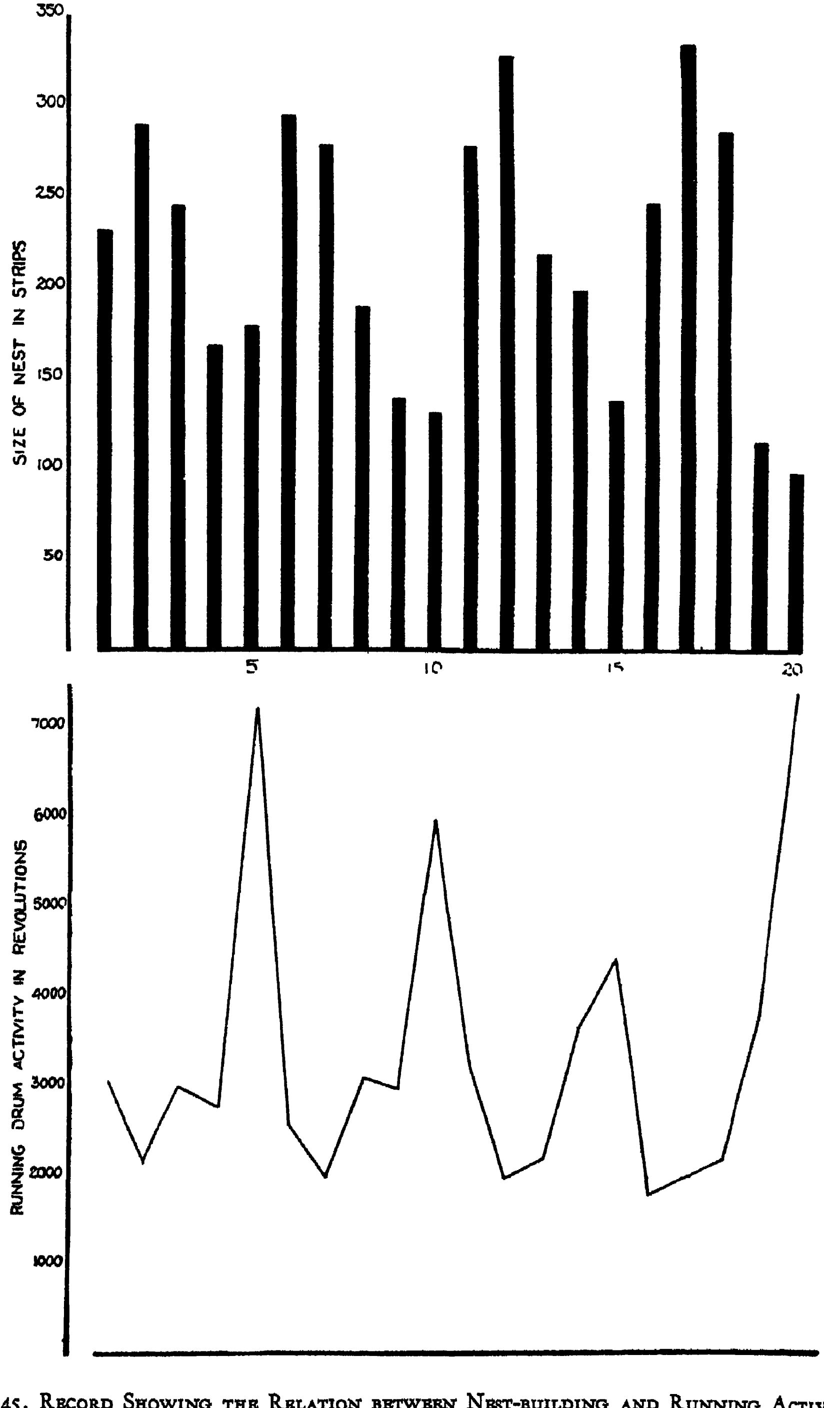


FIG. 45. RECORD SHOWING THE RELATION BETWEEN NEST-BUILDING AND RUNNING ACTIVITY (After Kinder)

we consider the growth of fat and hair during cold weather a part of the more primitive physiological manifestations of heat conservation. Nest-building, like the building of shelters and the wearing of clothing, is a much more highly developed method of maintaining a normal body temperature, but it is nevertheless an expression of the same impetus that pro-

FIG. 46. MULTIPLE ACTIVITY CAGE

duces the increase in fat and hair in more primitive animals (Martin, C. J., 1901). The mechanism of the drive involved here, therefore, is very different from that present in either the hunger or the sex activities.

Allied to nest-building in the rat are probably burrowing, the tendency of the animal to wedge itself into small spaces with contact on all sides, and its desire to huddle together with several of its mates. These activities also tend to conserve heat, in contrast to running, climbing, and jumping, which contribute to the maintenance of a constant body-temperature through heat production.

The various performances which, although associated with other drives, may be considered as contributing to the heat-regulating process, can be grouped as follows:

Nest-building Burrowing Huddling into small spaces Huddling together—social contact	} conserve body heat
Running Climbing Jumping	} increase heat production

Thus far we have investigated the different activities of the rat separately under more or less isolated and controlled conditions. We believe that it is possible, however, to study the animal under normal conditions, when it can indulge in any of the activities present in its usual outdoor environment. For this purpose we have constructed the set of cages shown in figure 46, in which a record can be obtained of the time spent each day by the rat in climbing, running, burrowing, gnawing eating, drinking, and mating. This cage makes it possible to account for the activity of the animal each day during every minute of the twenty-four hours. The large triangular central cage and all of the smaller cages at the side, except the revolving drum and the climbing tower, are supported on tambours. Running activity is recorded both graphically and with a cyclometer; climbing activity, by counting the number of times the animal goes up and down the tower each day. Both the entrance to the

tower and the top part are supported on tambours, so that a record is made on smoked paper each time the animal starts up the tower and when it reaches the top.

Because of the fact that we had only one cage we were not able to gather enough data to be of statistical value, but we have made sufficient observations to know that with some refinement of this method the behavior of the rat can be thoroughly studied in the laboratory. Certainly with this type of cage we can obtain a normal environment for the animal, in so far as it has an outlet for most of its different drives, and if we can judge how normal the environment is by the type of rat that it produces, the success of the method is unquestionable. An individual brought up in the multiple cage is far more intelligent than one raised in the ordinary running cage. Within the multiple cage the animal shows all kinds of constructive and imaginative activities, rarely, if ever, seen in an ordinary laboratory rat, and on occasions when it escapes it avoids recapture with extraordinary success. We may note in passing that were rats of this environment used for experiments on extirpation of the different areas in the cortex of the brain, much more noticeable defects in behavior might possibly be demonstrated as a result of the injuries than have appeared thus far in the rat kept under the usual laboratory conditions.

Individual differences are quite striking in the multiple cage if we may judge from our small number of animals. One rat will spend most of its time in the climbing tower, passing up and down as many as thirty or forty times a day; another will spend all of its time in the sex box; and another will gnaw all day long. None of our records have been taken over sufficiently long periods to permit us to give any perspective on either the constancy and fluctuations or the importance of the different activities in the life of the rat, but we do know that in this cage the running activity in the drum is reduced in every case to a few hundred revolutions per day. It is very interesting also, that in these cages where the animal has many different diversions the frequency of its eating period is greatly reduced. It enters the food-box once every five or six hours, and sometimes even less frequently, but whether it actually eats less food we have not yet determined.

That even the most complicated form of the rat's behavior may be studied in this cage is brought out by the following observations. In experiments on one animal a liberal supply of building material,—sticks, rope, stones, and cloth,—was placed in the large central cage. This animal had habitually deposited its feces in the water-cup. Usually the water was changed every day, but on one occasion, by some neglect, it was not changed for several days, so that the resulting odor became very unpleasant. At this point the animal started to cover the hole over the water-cup. It first removed part of the upper layer of the cardboard bottom of the large central cage, and dragged it into the water-box. It placed the cardboard over the cup and smoothed it down on all sides until the hole was perfectly covered. Then from the bottom of the central cage it lifted stones larger than its head three inches into the drinking cage and placed them over the cardboard cover. Besides the large stones numerous pebbles and sticks were used until the water-box was completely blocked. The animal had cut off its only water supply by this performance. Since we wished to see what it would do when it became very thirsty, the material was left undisturbed and no other water was given. After three days,

the animal pushed all of the sticks and stones from the drinking cage into the large central cage, tore up the cardboard seal, and drank its fill of the polluted water. This observation is certainly comparable to those made in the field. Had our apparatus been working better just at this time we should have obtained a complete biological record of this very interesting incident.

Another performance likewise constructive but less complicated was frequently observed. The rats plug up the entrance to any of the smaller cages whenever they have been frightened on entering them. This is the only explanation that can be offered for the frequency with which adult rats closed the entrance to the running drum shortly after they were placed in the cage. In one instance the opening was plugged up so tightly with nest-building material that a knife had to be used to open it up again.

Many similar examples could be given to demonstrate that in our artificially constructed environment practically every variety of behavior observable in a natural environment is obtained. And with a record of the way in which the animal spends its time before and after such episodes much more light will be thrown on their origin.

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THE CHIASMATYPE THEORY OF JANSSENS

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AMONG the many efforts made in recent years to establish a relation between structural conditions in the germ cells and genetic phenomena appears the case of Janssens' chiasmatypy as an explanation of "crossing-over" in *Drosophila* and other organisms. Morgan and his students have found the physical conditions, assumed to exist in chiasmatypy, suggestive of the mechanism required by the recombinations within the linked character groups observed in experimental breeding, and, so far, this is the only suggestion that has come from cytology to aid the geneticist in this significant problem. Just because of its importance in that application, the chiasmatype interpretation has acquired an interest much beyond what it would have had merely as an explanation of certain conditions occurring in the chromosomes during meiosis. It is true that, in its latest form, chiasmatypy becomes transformed into a theory that there are many ways by which, in one meiotic division, both equational and segregational separations may occur in the chromosomes; but this is merely an extension of the primary conception of Janssens that, in a particular manner, individual pairs of chromosomes may experience mutual interchanges of homologous elements. Since it is only in this more limited aspect that it has had extensive genetical application, it remains a conception which can be put to the test of direct observation on the chromosomes. It is proposed to submit Janssens' exposition to such an examination here.

By a most unusual coincidence the latest presentation of the case of chiasmatypy is based upon phenomena apparent in two genera of Orthoptera with which I have been intimately familiar for many years—*Mecostethus* (*Stethophyma*) and *Stenobothrus* (*Chorthippus*). Also I have studied with much care the cells of *Batrachoseps*, the form upon which the original conception was founded. This review is therefore incidental to a more comprehensive study, particularly upon *Mecostethus*, whose publication will supply many details which, although important to a thorough understanding of chiasmatypy, cannot be given here. Fortunately it is possible to resolve the complicated presentation of Janssens into a few simple elements, the consideration of which will be sufficient, I hope, to make a judgment possible.

ELEMENTS OF THE CHIASMATYPE THEORY

First, it would seem best to present the case as it was outlined by the author in his early paper. This may be done in the following statements:

1. There are certain phenomena in the first spermatocyte anaphase which are difficult to reconcile with the hetero-homeotype theory.

2. These suggest movements and translocations which involve the internal reconstruction of the chromosome.

3. If there were no such internal reconstruction of the chromosome there would be no occasion for two maturation divisions—a pure homeotypic mitosis,

added to a qualitative division, is entirely superfluous and without significance.

4. Added to this is the fact that maturation produces always four gametes, which, however, according to the hetero-homeotype theory, are of but two kinds. There seems to be no explanation of four gametes unless they are individually different.

5. There is no explanation of the pachytene stage by the hetero-homeotype theory.

6. The strepsitene stage is without explanation unless some change is accomplished during this long period.

7. While the hetero-homeotype theory supplies explanations for some phenomena of Mendelian inheritance, it fails in others because there are cases where there are a greater number of allelomorphic characters than there are pairs of chromosomes.

8. That which particularly characterizes the heterotypic chromosomes is their longitudinal cleavage in anaphase. Such a cleavage could not occur for various reasons given.

9. It is not probable that dyads (tetrads) come from a simple twisting of individual chromosomes, anatomically independent.

10. Various forms of chromosomes contradict the assumptions of the hetero-homeotype theory.

11. The alternative of a longitudinal division of the chromosomes in the metaphase of heterotypic division could not be realized under the conditions.

12. The only explanation consistent with the facts is one which realizes the occurrence, in one division, of both an equational and reductional division within the single chromosome.

As this summary indicates, Janssens' approach to a solution of his problem was largely from the *a priori* standpoint—to account for certain anaphase figures, to explain the tetraspore, to make understandable the maturation divisions, to make more applicable than the hetero-homeotypic theory does the phenomena of maturation in an interpretation of Mendelian heredity, etc., something must happen in the chromosome. In search for this peculiarity Janssens notes the strepsitene stage and sees in it a figure making possible the occurrence of both an equational and reductional division within one chromosome during a single mitosis. The relations of the homologous members of a chromosome pair, as found in the strepsinema, represent in a fundamental way the ones which are held to obtain in all the multitudinous forms of chromosomes in the phases of meiosis. This is represented diagrammatically by Janssens ('09) in figure 1, of which he gives this explanation:

We shall in this caption style as *dyads* a couple of chromosomes in strepsinema a little before the time of formation of the spindle, Schema I, *dyad*, C, *chromosomes*. We shall call *filaments* F the two chromosome-threads resulting from a longitudinal cleavage of one of them. The place where the two chromosomes of the dyad cross we shall designate as a *chiasm* or *knot* N; a *loop* or "*internode*" B is formed by the two chromosomes between two knots; finally, a *segment* is the part of one chromosome included between two knots or chiasms.

Although it is not thus stated in the description, the diagram is so constructed

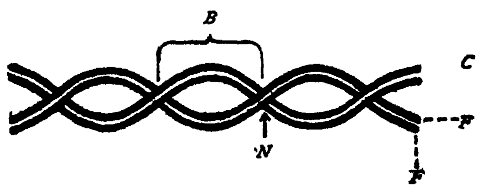

FIG. 1. THE BASIC FIGURE IN JANSSENS' PAPER, WHICH IS DESCRIBED IN THE ACCOMPANYING CAPTION

as to show that while the two chromosomes twist about each other, their chromatids ("filaments") lie as though projected in a single plane. Unless there were such a differential orientation, there would be no fixed positions for the chiasms, for these would be mere chance optical effects depending upon the point from which the twisted threads are viewed. It is not apparent, however, in any consideration of this matter by Janssens, how this precise arrangement is brought about.

Even if, for the moment, this matter of a specific and differential orientation is disregarded, there still remain a number of pertinent questions regarding the significance of the spiral condition in the

chromatin thread. Is it characteristic alone of the prophase stage of the first maturation, or is it a common disposition of the chromatin in prophase? If it is not unique in meiosis, what modification occurs that makes it so at this time?

In answer to the first question it must be said that the spiral form of the chromosome is a common condition of the prophase and appears to be the resultant of the rapid elongation of a thread within a limited area. The spermatogonia of the Orthoptera show very beautiful examples of spirals, as has been described by Sutton, Pinney, Wilson, Wenrich and others. In such cells the chromosomes extend across the nucleus and their ends are fixed at opposite sides. Under these conditions any increase in the length of the chromosomes must be compensated for by some change in the direction of their mid portion, often within a tubular vesicle. Mechanically, when a flexible rod is thus involved, there results a spiral figure, and that is what we find in Orthopteran spermatogonia. It is difficult to imagine any special significance in this particular spatial arrangement of the chromatin thread.

Janssens, however, sees in the first spermatocyte a condition which renders the strepsinema of highest importance for there, he assumes, two spirals twine about each other. How this relation is accomplished in such a manner as to be significant in the production of chiasms is not fully explained. Indeed, in his work on Orthoptera, the strepsitene condition seems to assume a minor rôle. It is not raised as a topic for discussion in the part dealing with *Mecostethus*, it is mentioned as a stage in the spermatogonia of *Chorthippus* but with no reference to its significance, and it does not appear as a topic in the outline of the general discussion. Among the very numerous diagrams explaining the assumed permutations of the chromosome parts ('24) only a few, mostly among the later ones, show the long familiar twisted threads. A careful examination of these, moreover, betrays the fact that some have taken on a new aspect and, instead of representing two intertwining spirals, merely show two superimposed split threads zig-zagging back and forth over each other in simulation of the strepsinema (Diagram IV). Even in the original presentation of the theory ('09) aside from figure 1 we see no more of the twisting pair of split threads, curiously placed so as to show the loops and splits in one plane, but instead a connected series of rings placed successively at right angles one to the other (Diagram XI). This is also the case in the paper of 1919 (Diagrams II, III) the only representation of the original conception being a figure copied from Wilson.

JANSSENS' EXTENSIONS OF HIS THEORY

In this preliminary paper we are promised, by inference, an explanation of how these "profound modifications of inner structure" are produced, but no convincing demonstration appears in the voluminous discussion of 1924. One is forced to conclude that the strepsitene condition gradually lost its suggestiveness and was replaced by another which had as prime features the following elements: (1) Any two homologous chromatin threads coming in contact may fuse and produce chiasms, permanent or transitory; (2) these contacts may occur face to face, in which event fusions may form between both members of the split threads, or edge to edge, when a chiasm is produced between only two of the four threads; (3) these fusions almost never take place immediately at the ends, but commonly near the proximal end; (4) by subsequent breaks at these points of permanent fusion,

new combinations of chromosome elements are made by exchanges of homologous parts; (5) these altered chromosomes are passed into the mature germ cells to become functional members of the nuclear mechanism. According to Janssens' own statement

> These segments, *and this is the very essence of chiasmatypy*, [my italics] interchange between allelomorphic chromosomes. These exchanges are made during the various stages of the maturation mitoses. ('24, p. 252).

The primary conception of an internal reorganization of homologous chromosomes by an interchange of like parts is maintained, but the method of its accomplishment is differently conceived. As the second sentence of the above quotation shows, the time at which chiasmatypy takes place has been extended to include the whole period of the maturation mitoses. This same idea is expressed elsewhere in these terms ('24, p. 258):

> We therefore often see, and at very different periods, chiasmatypies, complete as well as incomplete, indicated or finished. We draw from them no conclusion as to the exact moment when chiasmatypy begins or is completed. It is evident to us that it is produced at variable periods of meiosis and that there is no one moment peculiarly favorable for its production.

Finally, quite carried away with his idea, Janssens takes the final step and announces that any differential division, as between the equational and segregational form, within one mitosis is essentially chiasmatypy. Thus, in summing up the work on *Mecostethus* ('24, p. 196) he says:

> The two cases are not, strictly speaking, chiasmatypy, but they prove that the same mitosis may be, although for different chromosomes, at the same time equational and reductional, and this is the very essence of the theory which we defend.
>
> Thus we shall consider that very important fact from this point of view. It is moreover the first time that it has been pointed out.

As in so many other instances, Janssens quite overlooked previous announcements of his discoveries. The occurrence of equational and segregational division of different chromosomes in one meiotic division was described in the Orthoptera in 1905 (McClung), was demonstrated very fully by Wenrich in 1916, and was, at least by inference, described by Montgomery (1906) and by Wilson (1912) in the Hemiptera, where the X-chromosome divides sometimes in Meiosis I and sometimes in II.

Thus the original belief in a particular kind of internal chromosome reconstruction, by means of chiasms between twisted threads (as an explanation of peculiar conditions of first spermatocyte anaphase chromosomes and to meet certain theoretical difficulties of the hetero-homeotype theory), becomes a theory to explain any sort of combined equational and segregational action of a single mitosis. Notwithstanding the extension of the theory in this way, the principal basis still lies in the original figures of the first spermatocyte prophase, and an estimate of its value can best be gained by a detailed examination of these.

DO CHIASMS REALLY OCCUR?

It may be said at once that if Janssens' primary assumption be admitted, namely, that crossing threads in first spermatocyte prophases represent real chiasms, then all his numerous figures are possible, although this is not the only alternative. To enter into an analysis of these multitudinous configurations would be a waste of time—the essential thing is to discover whether the optical effect, so clearly evident in the cells studied by most investigators, upon which Janssens' interpretation rests, accords with his conception. We are not to discover whether chiasms are physically possible, but whether they do in fact

occur as described. It is most truly in this case not a theory but a condition that confronts us. Put concretely, the question becomes: "Do the structural elements of the maturation chromosomes, after they have become defined in the first spermatocyte prophase, maintain their integrity, or are they broken up and subjected to chance reconstruction?" In considering the problem, the fact, established genetically, that there is a reconstitution of the material units of hereditary processes must not unduly influence us, for the question at issue is not whether such changes happen, but, specifically, whether the mechanism described by Janssens is the one which actually exists. The test is, therefore, objective and observational and not speculative in character. It involves the use of the finest discriminative judgment in the interpretation of microscopical images, backed by a wide knowledge of the range and character of form variations of the chromosomes within the type of cells studied.

Janssens' knowledge of Orthopteran germ cells was apparently derived very largely from personal familiarity with only the two species described in his paper. The paper was written with slight reference to the large amount of literature on Orthopteran spermatogenesis and when notice is taken of this it is commonly in the form of notes which modify slightly, if at all, the form of opinion already expressed. Among neglected items of great significance bearing upon the problem with which he was concerned, and which are matters of record, may be mentioned (1) the almost universal occurrence of telomitic chromosomes in the Orthoptera; (2) the demonstration that the atelomitic chromosomes of *Chorthippus* are unions of non-homologous telomitic ones; (3) the fact that fiber attachment is practically a fixed structural chromosome feature; (4) chance-segregation and recombination genetically demonstrated by heteromorphic pairs; (5) the relations of homologous chromosomes in the tetrads and the sequence of their division demonstrated by unequal pairs; (6) the simultaneous occurrence of segregational and equational divisions of different chromosomes in one mitosis.

In extenuation of the errors and omissions in the work of Professor Janssens, it should be noted that war time conditions made it impossible for him to become familiar with many of the investigations reported from other countries. Further, during the completion and publication of his long Orthopteran paper, he was seriously ill with the disease which later terminated fatally. The contributions of Professor Janssens to biology were extensive and valuable, and it is a pleasure to me to express here an appreciation of him. We all delight to do honor to the memory of one who so sincerely and industriously sought to advance our knowledge in a field beset with many difficulties. In the same measure that he himself critically strove to understand the message written on Nature's page, we may be assured, would he wish others to appraise and judge the record which he has left. Since the conception of chiasmatypy is entirely that of Janssens, no consideration of it can escape an evaluation of the objective evidence he presented or of the attitude and methods which were his. Since the propounder of the theory can no longer defend his position I shall do my utmost to see that his views are correctly presented.

DIFFICULTIES OF INTERPRETING MICROSCOPICAL OBSERVATIONS

Admittedly, the conditions present at the time when the presumed changes of chiasmatypy take place are the most

difficult of interpretation of any found in the history of the germ cells. This is true in all cases. Even the comparatively large cells of the Orthoptera are really small bodies. Within these their very much more minute parts pass through most complicated evolutions. We are endeavoring to form a coherent picture of processes rendered static in their various stages. This would be hard enough for objects of ordinary size, but when it is attempted under a magnification of 3,000 diameters, with light passing through the masses instead of being reflected from their surfaces, and with only slight stereoscopic effect, it becomes exceedingly difficult. Within the narrowly limited mass of the cell lies its spherical nucleus, and in this space 23 chromosomes are distributed in such a manner as to approximate an even distribution in the first spermatocyte prophase. Naturally they present different aspects, according to their position, and often they overlie each other. Viewing the nuclear sphere with its constituent chromosomes, the observer must interpret the picture of two dimensions in terms of three. In diakinesis the formed chromosomes have much the same individual configuration as they show in the immediately subsequent metaphase, but at this time their chromatids are clearly distinguishable. Here Janssens found many of the figures upon which he based his views of chiasmatypy. It must always be remembered that when the fine, closely placed threads seem to intersect it is a matter to be decided, not directly observed, whether they do or not. To some extent the stereoscopic vision of modern binocular microscopes adds a measure of observational assurance to interpretation, but in the final analysis the judgment of the observer is the decisive factor. In the leptotene stages there is an apparently inextricable tangle of threads, but this becomes understandable when related stages are considered.

It is the great range and intricate character of chromosome movements, however, which renders difficult an appreciation of what actually happens within the narrow confines of the nucleus. A short, compact chromosome of an anaphase becomes first a vesicle with its chromatin uncertainly distributed and then a thin moniliform thread of relatively great length. Accompanying these physical changes are differences in reactions to stains which make identification of substances uncertain. Difficult as are the conditions there comes an element of assurance in judgments formed when the order and precision of movements are considered. Through the wide extent of plant and animal cells that have now been studied, the same procession of changes, individually varied in detail, to be sure, presents itself. We are confident of the reality and extent of the phenomena, but less assured of our intimate knowledge of them.

Partly this is due to an imperfect appreciation of the exact physical state of the materials whose set images we study. The undoubted gels and sols become translated in our thinking into the solids which the technique preserves in our preparations. We know now, even at this stage of microdissection studies on cells, that the protoplasmic differentiations which appear in their parts are not solids, but active, flowing, streaming and diffusing colloidal aggregates. Only when we think in the actual terms of physical structure can we appreciate the real character of cellular phenomena.

There comes, therefore, the need of translating in our thought the fixed pictures of apparently solid structures, into the real images of living, moving cellular elements. The chromosomes, which sometimes seem to stand apart from

nuclear connections, must be visioned as denser centers within a continuous medium. In most stages of meiosis the substance of the chromosomes merges gradually into the karyoplasm with varying gradation—only in metaphases do they present sharp limits. Even here, in preparations of highest technical excellence, their continuous relations are observable, and the dimensions of the chromosomes vary within narrow limits according to density and character of stain.

The outstanding difficulty in the chiasmatype interpretation, however, is the one already referred to—that of picturing the relations of structure as they lie superimposed in the line of vision. The two dimensional figures which appear as Janssens' version of "chiasms" are exactly the same in outline as those of other investigators who see no evidences of chiasm but only crossing threads. What happens at the apparent intersection is not directly observable, but must be conceived by putting together images of the same related threads as viewed from different angles in many chromosomes. There must be such a consistency of image thus derived as would result if one could actually take out a single chromosome and view it from every possible point.

MANNER OF SPLITTING OF CHROMOSOMES

Contributing to misunderstanding also is the fact that Janssens fails to comprehend the true nature of the first spermatocyte prophase chromosome. To him it is not a tetrad but a dyad. (Incidentally Janssens' use of the term *dyad* for a geminus or bivalent chromosome is incorrect, since it signifies the number of chromatids in a chromosome which is in mitosis and not the number of chromosomes in a multiple.) At some time and in some way a longitudinal cleft appears, but the chromosome is still a dyad. About the time and manner of the appearance of the longitudinal split Janssens is very uncertain, as indicated previously in the quotation given on page 347 and in the following extracts from his paper published in 1924:

> Near the beginning of the diplotene stage one sees here and there, at certain points on the chromosomes, a longitudinal cleavage appear which corresponds to the cleavage in the prophases of the spermatogonial mitoses. (p. 182).
>
> . . . . these fusions ("permanent" fusions in the dyads of *Stethophyma*) are very primitive and they were already observed in chromosomes which do not yet show the slightest tendency toward splitting. (p. 184).
>
> Toward the end of the strepsitene stage one sees clearly a second cleavage appear in each of the branches of the strepsinematic couples. (p. 217).
>
> It is certain that in *Stethophyma grossum* the fusions at points of intersection are produced at a very young stage and one which corresponds to the leptotene in the species where the pachytene is observed. It is quite possible that in these cases we have a complete chiasmatypy on account of the chromosomes not yet having undergone longitudinal cleavage (which is produced, however, often in slightly advanced prophases). (p. 253).
>
> If we have not spoken of the formation of chiasmatypies at so early a stage it is not a reason for saying that it cannot be produced. W. Rees B. Robertson wrote the following sentence which, we believe, indicates the solution of the question and which is of a nature to permit us to agree perfectly: "My conclusions from the Tettigidae are that these spermatogonial chromosomes on entering synapsis are already split." p. 258. We must say in all truth that we have not yet succeeded in finding that before the pachytene stage (synapsis) the elements which conjugate are already split, but we admit willingly that it is thus in the subject studied by the author, and we find in this fact of "presynapsis splitting" a reason for admitting that incomplete chiasmatypies may be roughly formed before the pachytene stage. (p. 254).

Having failed to appreciate the character of the longitudinal split and being so strongly impressed with the significance of the spiral condition of the chromosomes at certain stages, Janssens quite overlooks the most important circumstance in the history of the meiotic chromosome, i.e., the

simultaneous existence of two planes of division at right angles to each other, *proceeding from opposite ends of the chromosome.* This relation was admirably and conclusively demonstrated by Wenrich in his careful study of the "selected" chromosome of *Phrynotettix*. In this species conditions are the same as in other Orthoptera except that certain chromosomes may be individually recognized, at all stages of meiosis, by peculiarities of form and behavior. Because of these circumstances depend the manifold forms of chromosomes found in meiosis I of animals and plants. These have repeatedly been described for many species and do not require extensive consideration here, but since an understanding of them is essential to a discussion of chiasmatypy a few of the more significant ones will be reviewed. I should first like to recall the case of the double *V*'s, so very evident, particularly in the Hemiptera. In these, the two splits, proceeding from opposite ends of

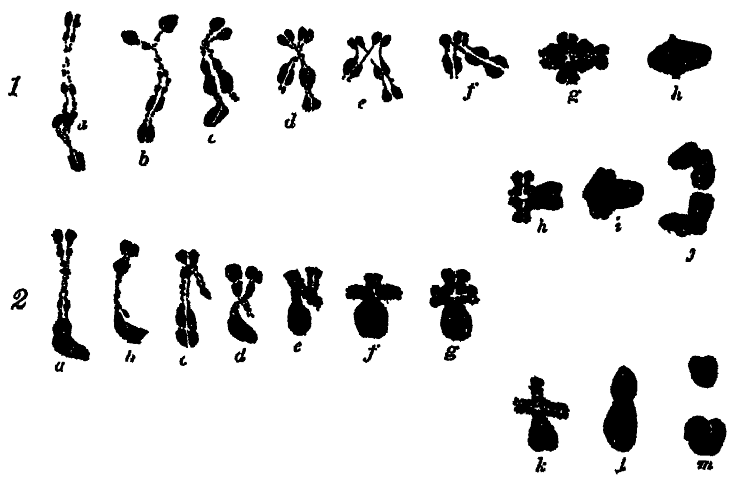

Fig. 2. Copies of Wenrich's Figures 64 and 65

Row 1 represents progressive stages of Chromosome "*B*" and row 2 of Chromosome "*C*." In each the simultaneous appearance of the two clefts in planes at right angles to each other, and proceeding from opposite ends of the tetrad, is shown. The tetrad 1*e* presents a typical "chiasm" which is nothing more than the crossing of one chromatid over another.

the two planes of splitting in the tetrad are distinguishable and it is established, for these cases, that the equational split proceeds from the proximal end (that at which the fiber attaches) to the distal, while the segregational proceeds from the opposite end at right angles to the first (fig. 2).

ORIGIN OF CHROMOSOME FORMS

Upon the relative rate and direction of the movements of the four chromatids in relation to these two planes of separation the chromosome, at right angles to each other, extend completely through its length. The chromatids, remaining united by their ends, diverge along each split for as much as 90°, producing a variety of figures. If one of these, which presents two divergences of 45°, be viewed exactly in the plane of one split, it looks like a simple *V*. Rotated through 90° it would appear again as a *V* but with the direction of the opening reversed. Any intermediate position would display both *V*'s, one from the outside, the other from

the inside. Whenever thus obliquely viewed each double *V* presents the appearance of two *V*'s with their inner arms crossing. Such crossed threads Janssens figures as representing a chiasm. Obviously, in this case, the two chromatids are not in contact and could not fuse, but the optical appearance is not thereby affected. It is only necessary to imagine the *V*'s compressed parallel to the axis of vision to bring the apparently crossed threads into contact. But why should movement occur in this chance direction instead of in a plane established structurally in the tetrad, which would reduce the double *V* eventually to a single *V* with double arms? This case illustrates the

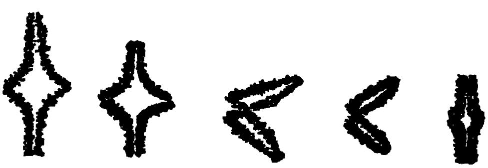

Fig. 3. A Copy of Paulmier's Figs. 1–5, Showing the Structure of the Tetrad in Anasa Tristis

Chromosomes 3 and 4 are viewed obliquely and present apparent chiasms.

essential weakness of Janssens' reasoning—it calls always for the operation of chance change against the inherent structural stability of the chromosome. While it may be regarded as extreme to instance the "chiasm" of the double *V* as illustrating chiasmatypy, the case does not differ in principle from the ones figured by Janssens (fig. 3).

From this double-*V* figure can be derived all of the various forms of the first spermatocyte chromosome by modifications of (1) the amount of separation of the four chromatids along the two planes originally at right angles to each other; (2) the relative time of the separations of these planes; (3) the amount of extension or condensation they exhibit; (4) the position of the fiber attachment; (5) the persistence or loss of the endwise union of chromatid pairs; (6) the spatial relations within these chromatid pairs. The question of chiasmatypy resolves itself accordingly into one concerning the interpretation of chromatid relations. Janssens chooses to assume that continuity of chromatid is lost and mechanical reconstruction accomplished through reciprocal exchange of homologous chromatid parts. A new organization is set up in the chromosome. There is no *a priori* argument against this, for all evidence indicates unique conditions at this period in the history of the germ cells, and genetic experiments demonstrate that an internal reorganization of the chromosome occurs after a manner explainable by chiasmatypy. But do the observable structural conditions of the chromosome support that view, or do they accord with the conception of persistent continuity of elements accompanied by spatial readjustments?

Before taking up the consideration of the different chromosome forms let us first note that movements, varied and extensive, characterize the chromosomes in all mitoses. There are separations and recombinations, twistings and loopings, diffusions and retractions, and all manner of combinations of these. Like so many living organisms, the chromosomes, by their own intrinsic contractile power, carry through their ordered movements. In our efforts to interpret the fixed stages of these activities we must always bear in mind the nature of the living substance and the character of its movements. The chromosomes are not rigid, immobile threads or rods, dependent upon external forces and chance contacts for their resultant forms, but active, autonomous elements pursuing an ordered course through a most involved and intricate series of

changes. We are not here concerned with the cause of these movements, but only with their manifestations. An understanding of them is, however, entirely dependent upon a true appreciation of the conditions under which they occur. These phenomena I have studied in many scores of Orthopteran species and have compared them with the ones appearing in most of the classical objects described in the literature. In particular I have for many years studied intensively the meiotic chromosomes of *Mecostethus* as found in the three species, *lineatus*, *gracilis*, and *grossus*, as well as those in *Stenobothrus* (*Chorthippus*) and *Chloealtis*, where euchromosome multiples occur. I am thus intimately familiar with the particular material upon which Janssens based his conclusions, and shall be able to criticize them, not through remote analogies with other and uncertainly relative conditions, but by direct comparisons. A brief account of the synaptic process in *Mecostethus* was published in 1924 and a more extensive and comparative study of meiosis in this genus will soon appear. For this reason the present discussion will be confined as much as possible to details most pertinent to the immediate issue of chiasmatypy.

CROSS-SHAPED CHROMOSOMES

Two first spermatocyte prophase figures, in particular, are used by Janssens as the basis of his interpretation—the cross and the ring. These are common forms of chromosome in prophase and metaphase of Meiosis I of both plants and animals and their correct interpretation has many times appeared in the literature, but both have been erroneously described in several instances. It remained for Janssens to give an entirely new and almost fantastic account of their structure. The cross (fig. 4), according to Janssens, results from the following chromatid movements: (Diagrams III, V, VI, VII, VIII, '24) (1) two homologous chromosomes, longitudinally split, approximate *side by side;* (2) the two chromatids, laterally in contact, fuse at some non-terminal point and

Fig. 4. The Formation of the Cross-Shaped Tetrad as Represented by Janssens in Diagram VI of his 1924 Paper

One homologue is represented in solid black, the other by dotted lines. A fusion between contiguous chromatids is assumed where the vertical line intersects.

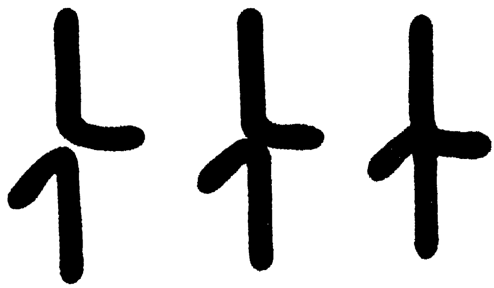

Fig. 5. Cross Formation as Represented by Janssens in his 1909 Paper, Diagram XVI

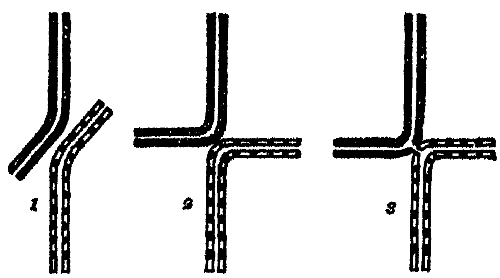

Fig. 6. Except in Details the Conditions Here are Similar to Those Shown in Figure 4

Copy of Diagram III of Janssens' 1924 paper

change their connection; (3) at the level of chromatid fusion the shorter arms swing each through 90° and come to lie at right angles to the axis of the longer members; (4) the longer arms may then

take a position in the same plane as the shorter, or not. A simpler method was described in the first paper ('09, Diagram XVI) (fig. 5), and again in 1924 (Diagram III). In this, two longitudinally split bent homologues unite laterally by their angles, where the chromatids in contact fuse and change their connections (fig. 6).

The result is the same as before—an exchange of equivalent segments between the homologous chromatids at the point of fusion. The diagrams given to illustrate this process are clear and convincing, but the accurate drawings of chromosomes in the assumed stage do not in any way support them. A study of these stages in the cells themselves shows nothing whatever to corroborate Janssens. I have examined hundreds of cross-shaped chromosomes, in all stages of development, not only in *Mecostethus* but in many other species, and I have never seen a single one which would correspond in its structure to the diagrams given by the Belgian cytologist. I have no doubt whatever of the error of his interpretation of this chromosome form.

Perhaps the best evidence as to the actual composition of the cross is given by the heteromorphic tetrads of *Phrynotettix* (fig. 2). It will be noticed that the chromosomes "*B*" and "*C*" may be constituted of unequal homologues, a circumstance which makes possible the exact identification of the two constituents. These are first seen lying parallel with each other, apparently unsplit, but shortly afterward a longitudinal division appears in each, beginning at the proximal end. Almost at the same time, the homologues diverge at the distal end, the shorter member leaving the longer. While the halves of the individual homologues produced by the division proceeding from the proximal end remain in parallel contact, the homologues move apart until they may lie extended in a straight line. The result is a cross-shaped chromosome with two splits intersecting at right angles—the one dividing both the small and large homologues rep-

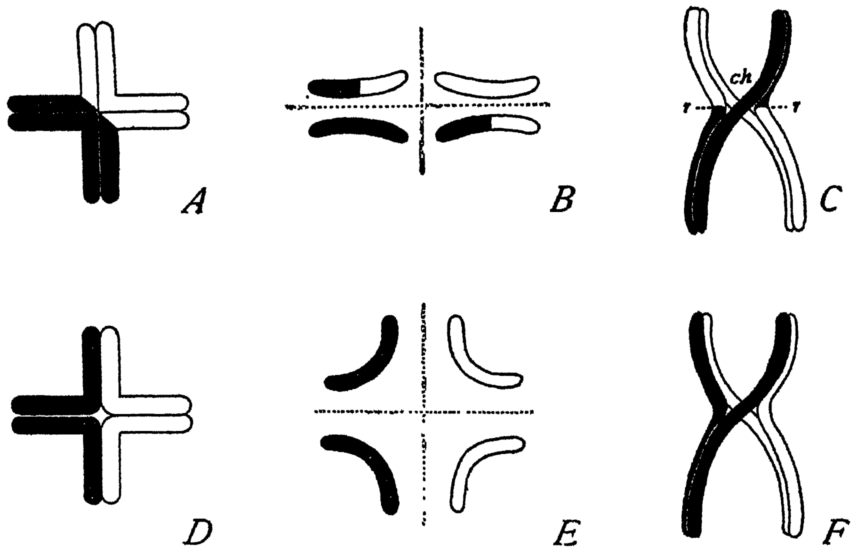

FIG. 7. WILSON'S FIG. 6 (1920) ILLUSTRATING THE DIFFERENCE BETWEEN JANSSENS' INTERPRETATION OF THE CROSS FIGS. A, B, D, AND THAT OF OTHER INVESTIGATORS, FIGS. C, E, F

resents clearly their equational division, while the other just as definitely marks the separation between the two homologues. In this case all the visible appearances confirm the interpretation, but Janssens, in discussing Wenrich's ('16) figure 62 of chromosome "*A*," disregards entirely the evidence presented for identification of the two planes, and, by substituting his own interpretation, distorts the figures into a support of his position. An oblique view of a tetrad in an early stage of the divergence of the homologues (Wenrich, fig. 64*e*) shows a double-*V* effect and the crossing threads, although evidently not in contact, become a chiasm to Janssens. Comparing the condition of the cross, as it actually appears, with Janssens' conception, these divergences may be noted: (1) the union of homologues is parallel and face to face and not at an angle and lateral; (2) union of chromatids is at the ends and not subterminal; (3) the chromatids continue unaltered from one extremity to the other and do not fuse (fig. 7).

An examination of Janssens' own figures in almost every case confirms the view opposed to his own (figs. 152 *c*, *d*, *e*, 183, 186, 187). The occasional instances of asymmetrical relations of the four chromatids at the center of the cross are easily understood and do not involve any breaking and recombination of elements. Those of the later first spermatocyte prophase, as in figs. 152, 153, are chromosomes still of a very loose structure in which none of the parts are clear and sharply defined. Those of the first spermatocyte metaphase, figs. 183, 185, 218, require more special mention because they afford a definite basis upon which to place an estimate of Janssens' judgment regarding conditions of chromosome structure. Fig. 183, chromosomes 6, 7 and 10, are quite symmetrical crosses viewed *en face* and give no suggestion of altered parts. Chromosome 5 of the same figure shows a very irregular and distorted appearance and obviously is not normal. Fig. 185, chromosomes 2 and 4 are clearly broken chromosomes such as may be found in any preparations that have suffered injury. Janssens recognizes their fragmented condition but, instead of appraising it properly, sees only an evidence that the break has occurred in a weak place which must be that at which the chiasm appeared. Chromosome 4 is broken not only at the presumed chiasm but also near the ends. All these clefts are beyond question pure artifacts. The long slender chromosomes of *Mecostethus* are easily injured in preparation and breaks of any character may be found. That Janssens should seize upon such obvious technical faults as evidences of fundamental reconstruction within the chromosome makes it very certain that his judgment of cytological values is not to be relied upon.

A similar demonstration of this fact is afforded by his interpretation of certain oblique views of first spermatocyte metaphase chromosomes. When they are viewed *en face* (fig. 182, chromosomes 1, 4, 7, 8, 9) or in polar view (chromosomes 16, 17, 18, 19) they are represented as perfectly symmetrical at the region of fiber attachment. Whenever they are represented in oblique view, however, their chromatid relations invariably are otherwise conceived, (chromosomes 2, 3, 13, 15, 21, 23). The drawings of chromosomes 21 *A* and *B* are revealing of the faults in Janssens' interpretation. Here a purely optical effect is converted into a structural relation quite alien to the real conditions as revealed by the history of the chromosome and by its appearance when viewed otherwise. This optical effect can be produced by varying the focus on any chromosome of homogeneous constitution and it differs according to the

angle at which it is placed in reference to the visual axis. But most convincing is the concordance between these chromosomes of *Mecostethus*, almost exclusively of one single type, as they appear in diakinesis, (with the four chromatids symmetrically placed in reference to the two prospective planes of division) and as they are later in the equatorial plate of the formation. It will be recalled that the process is a comparatively simple one in principle, as thus understood (figs. 8, 9, 10). The tetrad, at the beginning of diakinesis, is a rod, split longitudinally, in two planes placed at right angles. One of these represents the space between the homologous chromosomes of the pair, the other their coincident equational divi-

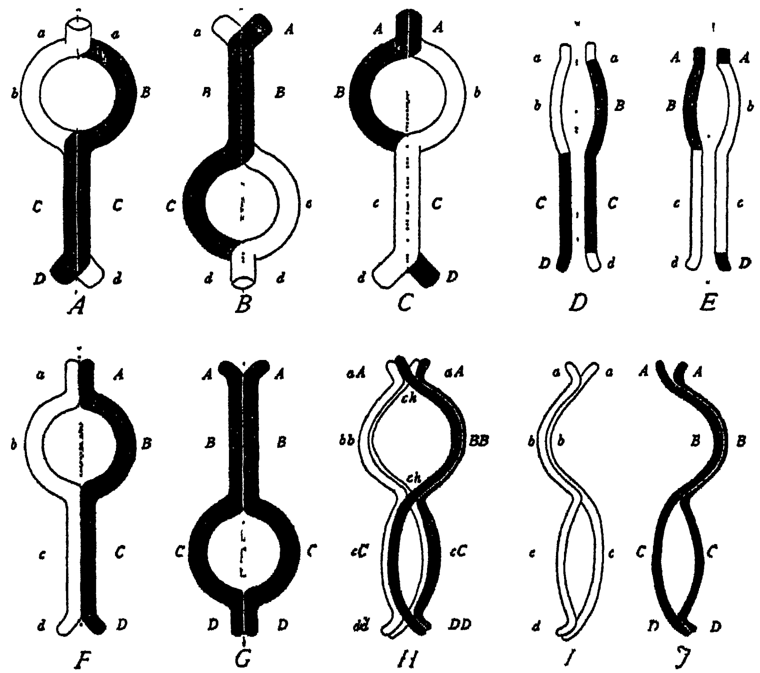

FIG. 8. THE DOUBLE RING TETRAD AS VIEWED BY JANSSENS, A, B, C, D, E, AND BY OTHERS, F, G, H, I, J

A and *C* are viewed at angles 180° apart, while *B* would represent the appearance at an intermediate position of 90°. At the points of intersection breaks are assumed by Janssens to occur, giving the results represented in *D* and *E* (Wilson's fig. 2 [1920]).

first spermatocyte metaphase (fig. 13. Janssens' figs. 186–191).

RING CHROMOSOMES

The ring chromosomes of the Orthoptera have been exhaustively discussed in many papers (McClung, '00, '02, '05, '14, '17; Sutton, '02; Wenrich, '16; Robertson, '08, '16; Granata, '10; Wilson, '12; and others) and a general agreement reached in regard to the method of their sion plane. This is a brief stage, but it is clearly apparent in *Mecostethus* and is of unusual prominence in *Stenobothrus*. Janssens does not figure it at all in the former genus and is not clear in the representation of it in the latter. *Mecostethus*, of all the genera of the Acrididae studied, shows the least tendency to produce rings, so that it is not a good form in which to work out their development, but *Stenobothrus* is exceptional in the clearness with which

the details of this type of chromosome formation are shown, especially in the case of the multiple euchromosomes. Robertson has represented these stages with great care and accuracy in a series of drawings ('16, figs. 163–177). The multiple ring chromosomes are of unusual interest because they show, beyond question, the alternate separation, in successive regions, of the four more or less parallel chromatids along the two planes lying at right angles to each other. Under ordinary circumstances, it is not possible to distinguish between the two lines of these chromosomes see no alteration in the composition of the constituent chromatids but merely alternate approximation and divergence between members of given pairs. Janssens' conception is radically different. For him, the series of loops in multiple rings in diakinesis represents persisting loops from the strepsitene stage, with chromatids breaking and fusing with different partners at the "chiasm." The position of the loops at right angles is not a primary relation, but one secondarily acquired. As a result of these altered relations, the openings of alternate rings,

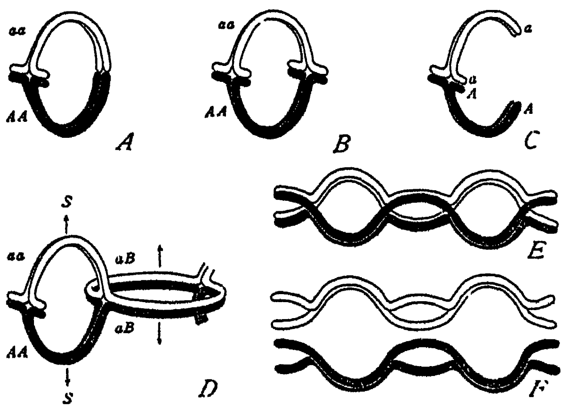

FIG. 9. THE STRUCTURE OF RINGS, SIMPLE AND MULTIPLE, AS CONCEIVED BY MOST INVESTIGATORS OTHER THAN JANSSENS (WILSON'S FIG. 3 [1920])

cleavage in a tetrad, but, in *Phrynotettix*, Wenrich was able to identify these definitely. The evidence here is that the two splits exist together and that separations of the chromatids in the two planes occur at the same time, but usually in unequal degree. Commonly, also, fiber attachment is so made that the first movements of the chromatids toward the poles of the spindle separate sister elements—an equational division. When chromosomes are long, multiple rings occur, and, as generally agreed, successive openings are placed at right angles to each other. With the exception of Janssens, observers of although in planes inclined at an angle of 90° to each other, are always the space between homologues and never between sister chromatids. In seeking a logical justification of this conception Morgan would assume that, e.g., the separation between paternal and maternal elements always occurs first and thus, as Wilson states, "makes the whole series of assumptions complete." But, as these authors imply, this merely adds another assumption to all those which have built up the chiasmatype structure. Unfortunately, it goes directly counter to the facts. As already pointed out in discuss-

ing the formation of the double *V*'s and multiple rings, the two clefts in the tetrad are present at the same time and proceed through the length of the thread or rod from opposite ends (fig. 11).

The cross and the ring are correctly regarded by Janssens as essentially the same in their formation—four chromatids, elsewhere divergent in pairs, approach and occupy a space equal to the sum of their diameters. The end of a ring chromosome or the place where two rings in a multiple join, if seen *en face*, appears as a cross (fig. 9). Viewed in this way such a chromosome should show one or more of the chromatids passing across from one side to the other, according to Janssens, but they do not do so and *none of his drawings of the actual chromosomes are shown in this position.* On the contrary, whenever chromosomes are thus figured with the four chromatids separate and visible, either in the first spermatocyte prophase or early first spermatocyte anaphase, the constituent elements maintain their positions in the same quadrants where they were found in the four strand stage. The only figures which may be regarded as even remotely supporting Janssens' position are those of broken, distorted or obliquely viewed tetrads.

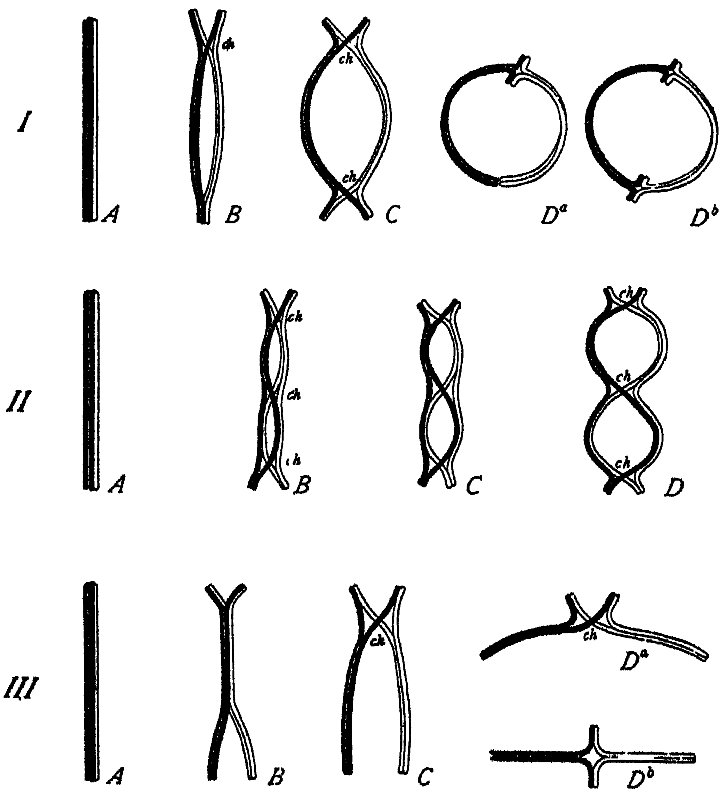

FIG. 10. METHOD OF RING AND CROSS FORMATION AS COMMONLY CONCEIVED (WILSON'S FIG. 5 [1920])
When obliquely viewed apparent chiasms, *ch*, appear in both forms. (Cf. III *C*, with 1*e* of fig. 2).

It thus appears that the chromosome forms most relied upon by Janssens as evidence for chiasmatypy are capable of

explanation in quite another and far more probable manner, which calls for no disruption of chromosome structure. Since this explanation was independently arrived at by a great many investigators, and since it is consistent with the structure of Janssens' presentation. The theoretical possibilities of movements between the four chromatids of a tetrad, assuming chiasms to occur, have been carefully and exhaustively explored by Wilson and Morgan in several publications. No better

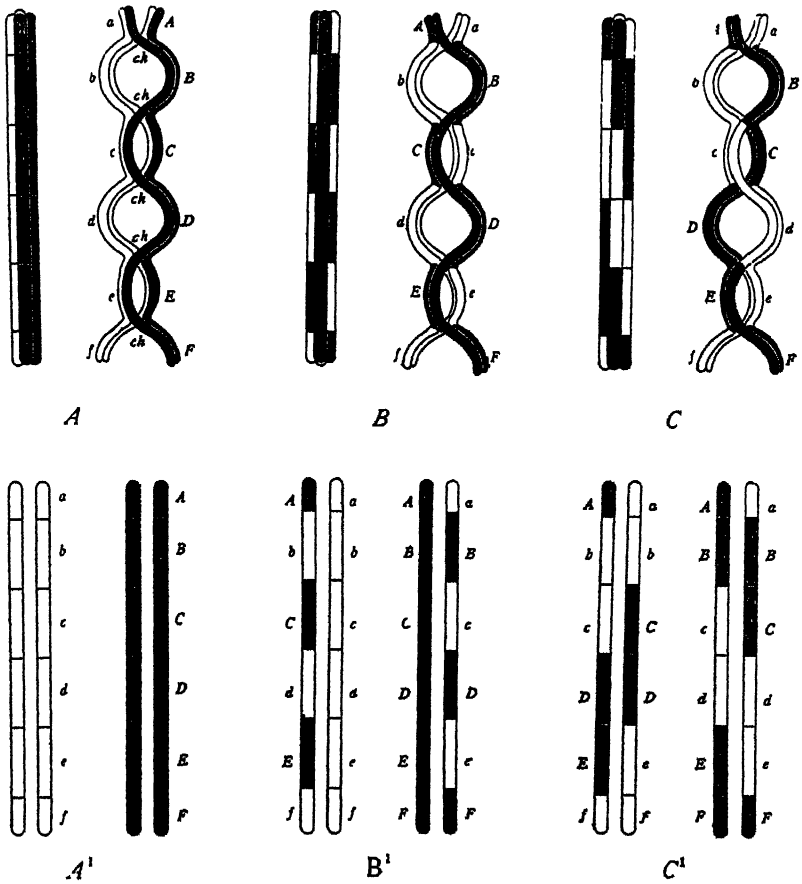

FIG. 11. MULTIPLE RING FORMATION AS COMMONLY UNDERSTOOD, *A* AND *A'*, COMPARED WITH JANSSENS' VIEW, *B* AND *B'*, *C* AND *C'* (WILSON'S FIG. 4, 1920)

In all these figures one homologue is shown in black and the other is white. Fusions and breaks at intersections produce, according to Janssens' view, the combinations shown in *B'* and *C'*.

of the chromosomes at all stages in their history, it must be assumed to be correct.

INADEQUACY OF EVIDENCE FOR CHIASMATYPY

It has been my intention in this review merely to consider the objective evidence for or against chiasmatypy in the light presentation could be given and it would be useless to encumber the literature by further considering what might happen under circumstances which do not exist. Because of the need to find a structural basis for the suggested facts of chromosome reorganization, as exposed by the

"crossing over" of characters in genetical analysis, Janssens' seductive suggestion required careful study. It has had its day in court and been found wanting. According to Morgan's latest conclusions ('25, p. 123)

> The genetic evidence may seem to indicate, and I think that it does indicate, the crossing over between homologous pairs of genetic chromosomes is, so to speak, a by-product of the reduction process. It does not seem to be one that necessarily takes place. It may not be an essential part of the reduction process and it would be unfortunate to press its claim at present into other fields, although there are clear indications that it does take place in other animals and some plants.

The present evidence is conclusive that it is not an essential feature of meiosis, for it does not occur in the male *Drosophila* although common as a feature of germ cell formation in the female. The presumed cytological proof for chiasmatypy, nevertheless, has been derived from studies on male cells. It is clear, therefore, that something more than physical conditions making possible mechanical interchange of chromosome parts is involved. No more favorable conditions for such translocations could be imagined than in the minutely attenuated chromosomes of *Mecostethus* in the forming leptotene, and presumably similar conditions obtain during the spermatogenesis of other forms, but instances of crossing over are rare or lacking in the Orthopteran male. Also, as indicated elsewhere, the obvious fact that during synapsis profound changes occur in the chromosomes, as indicated by the progeny of a single pair of parents, is no support of a theory which accounts for a particular kind of influence exerted after a specific manner. Evidence for the existence of change offers no argument for any one method of accomplishing it.

The term *chiasmatypy* was coined to designate the essential structural alteration presumed to occur in the meiotic chromosomes at a definite period of their development. It will merely confuse the problem for which the geneticists seek an explanation, to extend this idea of a structural reconstitution of the chromosomes, accomplished by a specific act, into a broader one which conceives any act of differential division in one mitosis as an instance of chiasmatypy. Janssens does this in his last paper, instancing, as already noted, the equational and segregational division of different chromosomes in one mitosis as the essence of chiasmatypy. Also he extends the period over which actual chiasmatypy may take place from first spermatocyte prophase to any period whatever of meiosis. In reality these extensions of the conception are just so many evidences of its original inherent weakness. Every step of the meiotic process has its own definite purpose—somewhere in this series the unique relations in life processes, which always mark the coming together of the maternal and paternal elements of the germ cells, are set up.

To those intimately familiar with the details of Orthopteran spermatogenesis it is quite clear that the basic condition upon which Janssens' conception rests, the formation of chiasms, has been entirely misconceived. The facts are otherwise than as reported—the "chiasms" are optical effects and not structural conditions. Thus we must conclude unless all other investigators are wrong and Janssens right. To the concordance of opinion in the past I must add the confirmation of my own judgment after extended and careful studies upon the same genera employed by the Belgian cytologist, backed by an extensive comparative knowledge of conditions in the Orthoptera as a whole.

THE NATURE OF THE CHROMATIDS

While, therefore, we must consider that the essential feature of chiasmatypy is due to a faulty conception resulting from misinterpretations of optical images, it is recognized that otherwise, with few exceptions, Janssens correctly represents in his figures actual conditions found in the cells. There are present the twists and turns of the first spermatocyte prophase chromosomes and the asymmetries in the chromosomes of first spermatocyte anaphase which first attracted his attention. How then can these be explained if not by the scheme of Janssens? To understand these conditions one must free his mind of many preconceptions regarding the physical nature of the chromosomes and regard them properly as living, active, viscous threads, exhibiting a wide range and varied character of intrinsic movements.

Also it must be appreciated that the unit in structure and movement is not a whole tetrad, or even its constituent homologous chromosomes, but the chromatids of which they are constituted. Herein lies another of Janssens' difficulties. For him there was something fixed and unchangeable in the tetrad unless by chance a break should occur and secondary connections between chromatids result. This is exemplified in a comment upon the interpretation of the multiple ring chromosome as represented in the figures of Granata, Robertson and others. The existence of twists, often asymmetrical or unequal, he regards as the best evidence against the view that such figures are produced by the opening out of four threads along planes at right angles to each other, for he says "the four filaments of a loop must be and remain parallel according to this supposition" ('24, p. 274). In reality the four chromatids, sometimes united only at their proximal ends, may exhibit almost all the configurations that could be imagined as the result of the somewhat free movements of this number of active, mobile bodies under the conditions set by the cell. In the later first spermatocyte prophase stages the extent of independent movement becomes much reduced and in the metaphase complete immobility appears to be reached in the apparently homogeneous chromosomes.

This state is succeeded with startling suddenness by movements in the anaphase which reveal at one time both planes separating the four chromatids (fig. 13, Janssens, '24, figs. 186–193). In this manner there reappear the conditions of diakinesis. Even in *Mecostethus*, where uniformity of behavior is more nearly reached by the chromosomes than in any other Orthopteron, there are sometimes asymmetries shown by twists of the chromatids (Janssens, '24, fig. 191). Such phenomena are much more marked in batrachians, and apparently were the primary incitement to the chiasmatype conception. According to Janssens, only by breaks and recombinations could such relations between formed chromatids be brought about. For this idea of fixity in

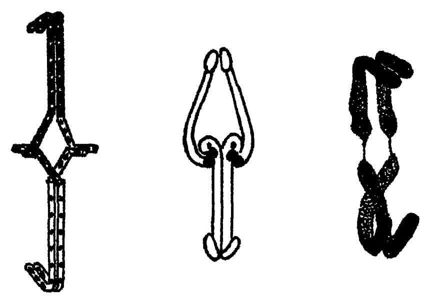

FIG. 12. COPIES OF DIAGRAMS XXIII AND XXVI *b*, OF JANSSENS' 1909 PAPER, AND FIG. 259 *y* OF HIS 1924 PAPER

Such appearances of asymmetrical relations in the chromatids of tetrads led Janssens to think of the breaking and recombining between chromatids in the tetrad.

condition, disturbed by uncertain and unpredictable accidents of contact and exchange, we must substitute the view which recognizes in the tetrad four separate, moving elements, which, at different first spermatocyte prophase stages, may variously orient themselves without loss of continuity or of primary relations. In this way all the curious and sometimes complicated chromosome forms receive ready and reasonable explanation. By its nature chiasmatypy could account only for relations between the parts of a single tetrad, but a proper appreciation of the real nature of the chromatids and their movements makes possible an understanding of unusual relations between whole chromosomes. Thus, annular chromosomes in the first spermatocyte prophase may interlock, and I have seen as many as three in a chain. Such interchromosomal adjustments could take place only between freely movable elements, just as they are, in like manner, broken before the metaphase, where they are never found.

An extensive review of late chromosome forms would hardly be appropriate in this place, but since consideration of these led Janssens to his views on internal reorganization of chromosomes it may be profitable to note a few typical examples. Diagrams XXIII and XXVI of Janssens' original paper of 1909 are representative of the conditions which so impressed him with the inadequacy of the hetero-homeotype theory and the need for a new interpretation. The first of these represents a view *en face* of an elongated early (fig. 12) anaphase cross with non-terminal fiber attachment. This condition is pictured in figure 259 *y* ('24). The lower limb presents a chiasm near the equatorial plate. Such a figure could result, argues Janssens, only by the fusion and recombination of chromatids at this point. In reality, all that has happened here is a rotation of the two chromatids around the lengthwise axis of the chromosome. The other diagram represents a chromosome of the same character in which rotation has occurred symmetrically, but in opposite directions, between the chromatids above and below the equatorial plate. This is a common condition in long chromosomes, such as the euchrosome multiples of *Chorthippus*, and like relations are represented by Janssens ('24) in figure 259 *e*, *j*, *r*, *t*. It is rather curious that Janssens, who was so much impressed by the rotation of chromosomes about each other in the strepsinema and in other stages, should so entirely disregard the evidences for similar movements between chromatids.

Such rotation of chromatids occurs also between the sister elements of spermatogonial chromosomes in the Orthoptera, and between those of somatic cells in a great many forms with long chromosomes, as for instance the Urodeles. The simulation of the assumed chiasms in such a manner is pointed out by Schrader and Schrader ('26) in *Icerya*, where the two haploid chromosomes are longitudinally split and spirally twisted. There can be no question here of confusing synapsis and splitting, for there is but a single one of each chromosome present. Nevertheless, just such figures as Janssens bases his views upon appear. (See Schrader and Schrader, text fig. 6 and fig. 11, Pl. VIII.) Every appearance of the chromosomal elements is suggestive of mobility and it requires little imagination to account for all the varied chromosome forms encountered in meiosis when it is realized that the chromatids have their own inherent powers of movement. The asymmetries on the two sides of the equatorial plate in anaphase chromosomes, which were instanced prominently by

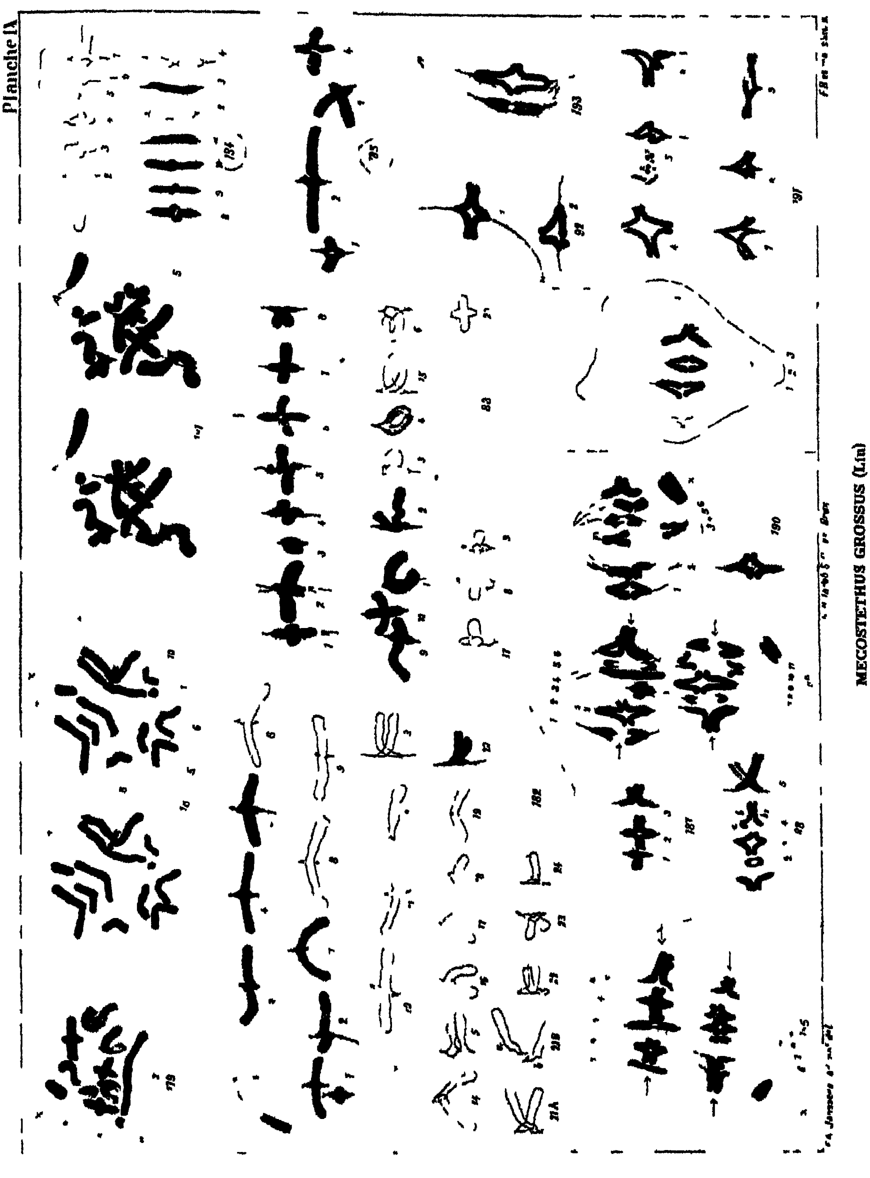

Fig. 13. Copy of Janssens' ('24) Pl. IX, Figs. 179–193, to Which Reference is Made in this Paper

Attention is called particularly to the exact concordance in the structure of the cross-shaped chromosome in metaphase, fig. 183, chromosomes 6, 7, 10, and in early anaphase, fig 186, chromosomes 2, 4, fig. 187, chromosome 2. Contrast these with oblique view of similar chromosomes, fig 182, chromosomes 13, 21, 23. It is of interest to compare the symmetrical appearance of the ring, fig. 183, chromosome 14, with chromosomes 13, 15, 16 of the same figure.

Janssens as evidence of profound internal chromosome changes, are nothing more than indications of this individual movement on the part of the chromatids. Diagram XXIII (Janssens, '09), is illustrative of this condition and will serve as an example (fig. 12).

THE STAUROSOME THEORY OF CHODAT

Recently ('25) Chodat has come to the support of chiasmatypy by describing in *Allium ursinum* the formation of reconstituted chromosomes which he calls "staurosomes." The basic figure here is the old familiar one of two bent chromosomes twisted about each other and joining laterally near the ends. No explanation has ever been offered for the constant establishment of just such relations, with overlappings symmetrically placed at the two ends of the chromosomes, and Chodat offers none. They just happen. Upon this event the ends diverge appropriately, the chromosomes split, exchanges between homologous chromatids take place at the point of contact, symmetry is established, and a split ring takes its place on the spindle. There is nothing new here except the peculiar configuration of the crossed ends of the two chromosomes and the same criticisms apply as in the case of similar figures given by Janssens. As I have taken care to point out on several previous occasions, it is rather significant that in the representation of such crossed chromosomes no one ever gives figures showing end views of the combinations. Always it is a side view that is represented. The reason for this is obvious to one who has sought for appropriate figures, for, viewed from this aspect, ring chromosomes show perfectly symmetrical arrangements of the parts and no such lateral displacement as would be required by Chodat's assumption. Curiously enough on rare occasions there do occur instances when tetrads take their places on the spindle with homologous chromosomes superimposed. In this case an end view sometimes shows the obliquity which would be required. One figure given by Janssens ('24) suggests this condition (fig. 13, Janssens' fig. 183, chromosome 4). Such exceptional cases, however, give no warrant for the disregard of the typical, normal state of organization in the tetrad, and it does not appear that the representations of the "staurosomes" by Chodat, and of similar figures by other authors, are based upon such real appearances, but rather are due to misinterpretations of optical images.

SEILER'S CRITICISM OF CHIASMATYPY

In a recent paper Seiler ('26) reviews chiasmatypy and from general consideration of germ cell conditions reaches a conclusion adverse to that of Janssens. While I do not believe that it is possible to evaluate correctly cytological evidence in the absence of personal familiarity with the material under discussion, it must be admitted that there is a conformity to certain general principles of behavior in all germ cells, and that accordingly it is permissible to call into question any interpretation which departs widely from the one grounded upon the consistent studies of many investigators. It is perfectly evident that the basic chromosome forms upon which Janssens based his conception—the cross and ring—are common structural conditions in a wide variety of plant and animal germ cells. On the ground of such a community of conditions it seems entirely justifiable to question views that are not concordant within the range of resemblances. From this standpoint Seiler's criticisms of chiasmatypy are of value. Taken in consideration with the

fact that they are in agreement with the views of practically all other students upon the subject, they acquire additional force.

PRELL'S THEORY OF RHEGMATYPY

Because this is specifically a review of the single conception of chiasmatypy, it does not seem desirable to consider at length theories of chromosome reconstitution based upon other phenomena than chiasm formation. There may, nevertheless, be a justification in referring to Prell's "rhegmatypy" in view of the fact that it does not differ in principle from some of the later modifications of Janssens' own views. Certainly when Janssens claims that internal reconstruction of the chromosomes may take place at any period of meiosis, and when he asserts that the segregational division of one chromosome and the equational division of another in one mitosis represent the essence of chiasmatypy, then this enlarged view embraces in effect all similar explanations. Accordingly it may be stated that in putting forward his theory of rhegmatypy Prell is, in principle, supporting the position of Janssens and even in the details of the mechanism involved does not differ from certain modifications of chiasmatypy developed in its last presentation.

Rhegmatypy is represented to be a process by which, the total amount of chromatin presumably remaining constant, fragmentation increases the total number of chromosomes as between species while combinations reduce them. The result is to produce, necessarily, different groupings of genes. Such reductions in number by unions of chromosomes is not a theory but has been clearly demonstrated in the Acrididae (McClung, '17). In *Hesperotettix viridis* there may be as many as three euchromosome multiples in one individual while another has none. *Chorthippus*, *Chloealtis* and European species of *Gomphocerus* show a permanent union of the same number of chromosome pairs. Fragmentation, increasing the total number of chromosomes in cells, has been described by Hance in the somatic cells of the pig. The experimental and cytological studies on *Drosophila* have shown that genetical modifications are correlated with shifts in the position of parts of chromosomes. Metz has indicated the relation between chromosome groups in various species of Diptera and has suggested the possibilities of unions and disunions of chromosomes to account for the seriations displayed. There are numerous obvious possibilities of such physical readjustments in terms of chromosomes and, in addition, it is more than probable that specific differences in chromosome numbers may result from intimate regroupings of more elementary chromatin aggregates. Unless it can be shown that there is some determinable system in such variations, our progress is not much advanced by giving new names to old facts.

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ANIMAL AGGREGATIONS

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I. INTRODUCTION

IT HAS long been known that animals may aggregate into groups or clusters, more or less closely associated, in which physical contact may, or may not, occur. Normally actual physical contact is found as a part of the aggregation phenomenon in many Protozoa, *Paramecium* for example; in flat worms such as the planarians; in earthworms; in arthropods and molluscs; and among many vertebrates, including fish, frogs, reptiles, birds and mammals. Among other animals similarly widely distributed through the animal kingdom aggregations occur in which constant physical contact is not normal. These may be illustrated by the swarms of gnats that dance together like animated particles; by ants, bees, schools of fish, flocks of birds, herds of ungulates and groups of various other mammals, including man.

These two types of animal aggregations are not mutually exclusive, for the animals under consideration may show first one and then the other in different phases of their life or seasonal cycle. Thus honeybees, though colonial, are normally out of physical contact with their fellows; and yet during swarming and in cold winter weather, they aggregate in dense clusters in the closest possible physical contact. Ants and other animals behave similarly.

There are also abundant cases of more complete change in the reactions of animals toward each other; they may lead wholly or partially solitary lives during part of their seasonal or life cycle and come together in flocks or in actual physical contact at another period. Such is the case with the grackles, which nest under separate conditions and then join in large flocks during the migration, or with deer, which summer separately or in partial family groups and then winter in herds, or of frogs, which remain practically solitary during the year, except for possible hibernation groups, and then aggregate during the breeding season, or of land isopods, which congregate into dense bunches on the approach of certain adverse conditions.

The aggregations of the physical contact type are of necessity transitory in character in motile organisms, while in sessile animals, such as the ascidians or the marine mussels, this may well be the normal way of living. The physical contact type of aggregation finds its most complete expression among the sessile colonial organisms that grow in dense stands, consisting of many individuals physically connected with each other throughout life. Hydroids of *Obelia* represent this growth form.

The aggregations of the non-physical type, that is, the flock or the herd, may be constant and normal for some species. This is usually spoken of as the social habit. It finds its best expression in insects such as the ants and termites, among whom polymorphic forms have evolved that do not complete their sexual development, but serve the colony in other specialized capacities.

Animal aggregations may be classified

on many other bases besides that of the degree of physical contact. Deegener (45) has made an exhaustive classification of the different forms of animal groupings (*Vergesellschaftung*) in which he undertakes to arrange logically all such associations, ranging from the relatively simple colonies of *Synura* or *Charchesium*, where all the individuals are similar, all arise from the same parent cell, and all are organically connected with each other, to colonies of ants with their complicated social structure, which may include their slaves, their commensals, their tolerated guests, parasites, parasites of the parasites, etc.

Deegener's primary division is into "accidental" and "essential" societies. The distinction is made on the basis of the supposed usefulness of the grouping to part or all of its members. Unfortunately this major division is made as a result of observation and speculation only and must be revised as the field is attacked by modern experimental methods.

It is of decided interest to us to find Deegener recognizing all such groupings in the animal kingdom to be aspects of a single series of phenomena, the more highly developed of which we have been accustomed to regard as making a separate category of relationships which we have designated as social.

Deegener's first subdivision is on the basis of the composition of the group: homotypic, if it is made up of representatives of a single species; heterotypic, if representatives of more than one species are present. Then come divisions based on such criteria as whether or not the members of a colony are organically connected; whether they are grouped together from the beginning of their life or come together later; whether all or only part of the animals benefit from the association. Finally come distinctions based on the particular factors that cause the group to assemble. Thus among the "accidental" aggregations we find "Synchoria," which occupy the same place; "Synchaemadia," which over-winter together; "Sympedia," which are groups of offspring of the same mother; "Symphagia," groups that cluster about the same food, etc.

Deegener apparently would classify the animal association of modern animal ecology as a "Heterosynchorium," since it is composed of several species occupying the same place without the individuals making the group being of obvious advantage to each other. He does not recognize the existence of such an association when some of the animals are benefited.

An ordinary ant colony, considered only in regard to the ants themselves, he would class as a "heteromorphic gynopaedium," which means that it is composed of unlike individuals associated with their female parent; a termite colony becomes a "polymorphic patrogynopaedium," since both sexes are present with their polymorphic offspring. These examples will suffice to show the extent of the classification, and the expressive and correct, but cumbersome terminology proposed.

In the present paper we are primarily interested in those groupings of free living, motile animals that come into close physical contact but are not obviously and intimately integrated into a social unit. In other words our main attention will be fixed on what Deegener regards as "accidental" rather than "essential" associations, but without including sessile colonial forms. Such aggregations may be spoken of as congregations, groups, clusters, or bunches, with various shades of meaning. The term aggregations is purposely used in a large, loose sense to cover the whole range of phenomena to be discussed.

It will not be possible to extend the scope of this paper to include all phases of the aggregation reactions of spermatozoa and of swarm spores of plants, about whose activity a large literature has developed (120). They exhibit to some extent many of the phenomena to be discussed later.

II. METHOD OF FORMATION OF AGGREGATIONS

1. *Tropisms*

The method of formation of aggregations excited much attention in the three decades from about 1888 to 1918. One group of investigators, headed by J. Loeb (122) were chiefly interested in the phenomena concerned with forced movements. When exposed to certain stimuli some animals react as though they were automatons forced by the interaction between their own organization and their environment to move in certain directions and thus to aggregate when available space is limited. Such reactions were originally spoken of as tropisms and may well be illustrated by the reaction of the larvae of *Arenicola*. Mast (129), who has been consistently critical of interpreting any animal reactions as approaching automatism, says: "There is no trial reaction in this process." The movements appear little more voluntary than the precise movement of algal swarm spores. Under these circumstances the larvae aggregate automatically if space near the light is limited.

Galvanotropism frequently yields aggregations in as diagrammatic a fashion (122).

2. *Trial and error*

On the other hand animals may congregate as a result of a series of reactions which suggest the human method of "trial and error," as described by Jennings (109) or, as Holmes has put it (94) by the selection of random movements. The classic case of this sort of aggregation is that described originally by Jennings, when paramecia collect in a more acid portion of the water they occupy. This kind of reaction is so well known as to have been diagrammed by all the current textbooks of zoology. It is worth emphasizing, however, that such a method of formation of an aggregation is not necessarily less mechanistic than is the type of reaction given by the larvae of *Arenicola*. It is also of interest to us that as the paramecia aggregate, the carbonic acid given off as a result of their normal metabolic activities tends to keep the region more acid and thus to perpetuate the aggregation

When there is a limited amount of space available, or a limited amount of optimum space, aggregations may form from either of these two reaction methods, depending in part on the nature of the stimulus emanating from the favorable locality, but in the main on the reaction system of the animals involved.

If the conditions are such that directive stimuli are absent, aggregations, if formed, will result only from the method of "trial." This apparently happens many times in nature and in the laboratory. Thus coccinellid beetles form hibernating aggregations (13) under protecting rocks and land isopods will gather (4, 7) about a small inequality of an otherwise homogeneous substratum of filter paper. Isopods readily do this when they are in darkness and probably find the inequality only by the sense of touch in random exploring movements. To animals of more highly developed nervous systems such places as the shelter of a rock or an inequality of the substratum, if perceptible at a distance, may serve as a sign of favorable conditions to which the animals would

then react (129). With animals on lower levels of nervous development, and certainly with isopods in the dark, the reaction must be a direct one to the immediate individual experience.

Such behavior as we have been discussing is obviously the result of the reactions of animals to their physical surroundings. As will be seen later, in the absence of elements usually found in the normal physical environment, animals may so react to each other as partially to substitute for the normal environment; that is, other individuals may take the place usually occupied by non-living environmental items. Three types of explanation have been advanced for this kind of phenomenon, two of which imply some innate social tendency, and another which explains such aggregations in the same terms we have already been discussing. These may be taken in order.

3. *Wallin's Prototaxis*

Wallin (203) has postulated a tropism which he believes to be of fundamental importance in the reaction of cells of multicellular animals as well as of animals in general. This tropism he designates as "prototaxis." Now a tropism may best be understood as being a reflex action of an entire organism. Animals or cells exhibiting prototaxis are supposed to have an innate tendency to react so that they form aggregations (positive prototaxis) or so to act as to remain solitary (negative prototaxis). When one examines this tropism he finds that unlike most, it is a compound affair due in part, according to Wallin's account, to chemotropic reaction. We also know that thigmotropic behavior is also frequently concerned. In fact this "tropism" becomes very much like the type of reactions usually referred to as instinctive by older writers, except that no one would have called the reaction of

4. *Instinct*

Deegener, both in his earlier studies (45) and in later ones (46, 51), concluded that aggregations are caused by the presence of a group, or social, instinct. Thus he comes to the same unilluminating conclusion reached by so many of his predecessors in this field.

The question immediately rises as to what social instincts may mean. Szymanski (197) undertook to investigate this problem by comparing the reactions of isolated caterpillars of *Hypnomenta* and *Arye* with those given by groups of caterpillars placed in the same general region. He believed that one can recognize reactions in the group similar to those given when the animals are alone. These he would designate as primary reactions. It follows that reactions given in the group that differ from those of isolated individuals must be due to the interaction of different individuals on each other. This he would call secondary or social behavior. This is the development of a similar idea held much earlier by Tarde (198).

5. *Aggregation by individual rather than social reactions*

Szymanski found that the factors causing the aggregations of caterpillars under experimentation were, first, the crowding of many individuals into a small space; second, tropistic reactions; third, the differential reflexes depending on whether the anterior or the posterior end is stimulated; and fourth, the method of locomotion and feeding. He thinks that groups are formed as the result of the primary individual reactions, not of the secondary social ones, at least in the cases studied. He deprecates, rightly, the tendency to emphasize social instincts as factors in colony formation when it is

nomena otherwise. Krizenecky (114) came to similar conclusions.

The observations on water striders (67, 104, 164), *Notonecta* (35), *Belostoma* (181), and frogs (40), as well as the tremendous literature on general animal behavior to which reference has already been made, indicate that aggregations do form in many cases without evidence of a positive social instinct. Thus it will be unnecessary to assume a social instinct or urge in order to account for the formation of many of the animal aggregations to be discussed. The only social trait necessary in many cases is that the animals shall be willing to tolerate the close proximity of other individuals. Once formed, aggregations may remain for some time merely because of lack of disruptive stimuli.

III. GENERAL FACTORS CONDITIONING AGGREGATIONS

In many animal species the formation of aggregations depends on the physiological state of the animal (63). This may be controlled by internal developments, such as the maturing of the sex products, or by external factors, as when land isopods are made to bunch by controlling the moisture of the substratum; but more commonly the internal and external factors are closely combined. Some of the more outstanding of these conditioning factors are discussed.

1. The breeding season

a. Water isopods. My own attention was drawn to the general problem of animal aggregations while studying the factors controlling the rheotropic reaction in the common water isopod *Asellus communis*. As spring came on the stream isopods no longer gave highly regular, positive response to the water current but might strike across a strong current, guided apparently by sight, and seize another isopod, male or female. From such a beginning one might soon have all the isopods under observation gathered into a compact rounded cluster, rolling over and over in the water.

During the height of the breeding season stream isopods disregard the stimulus of a water current almost completely unless they are isolated, and even then they frequently fail to give the usual response. On the other hand, I have repeatedly tried to induce half-grown Aselli to form such a cluster, even placing them in a vessel with rounded, smooth bottom where they were continually brought in contact with each other, but no real aggregation resulted. Bunching may be induced in adults out of the breeding season, but many conditions that favor it in April during the height of the breeding season have little or no effect in late May (5).

b. Frogs. With the approach of spring, frogs desert their hibernation quarters for breeding places in the shallow ponds (40). Many hibernate in the mud at the bottom of these same ponds, but others winter elsewhere, perhaps in nearby bodies of water or on land among masses of dead vegetation or in localities similarly favorable. Cummins suggests that such frogs may migrate to open water caused by the early melting of ice in a pond with proper exposure. Banta (11) and Yerkes (216, 217) find evidence that frogs may respond to frog calls and splashings, particularly during the spring breeding season. Studies on the breeding migration of toads indicate that with them the voice serves as a sex call (36, 134).

Cummins (40) concluded as the result of his observations on a partially fenced pond that voice is not an essential inciting or guiding factor in the spring migration of frogs, since intense migrations followed periods in which there was no croaking in or near the pond, and on the other hand,

great vocal activity was not accompanied by increased migration. Certainly vocal activity cannot account for the migration of the voiceless *Ambystoma*.

The immediate inception of the migratory impulse must be intrinsic and is probably associated with the condition of the sexual glands. It is secondarily conditioned by weather, since waves of migration are coincident with high relative humidity and with a temperature of from 41 to 52 degrees F. The migration is independent of daylight. All the illuminating observations of Cummins still give no information as to why the frogs congregate in a given pond or how they learn of its existence. He does record that the migration routes are not direct, so that we may assume that we are dealing, in part at least, with random movements, probably largely controlled by temperature. Casual observations would indicate that the migration of *Ambystoma* is controlled in the same fashion.

During the breeding season a gregariousness appears among frogs which does not exist under usual circumstances. This is not entirely accounted for by the tendency which the animals exhibit to seek a similar habitat for breeding (96), for if there are only a few pairs of frogs in a given place, they force themselves together as closely as possible and the eggs form a continuous mass (72).

At the height of the breeding season several males will struggle for the possession of a single female (11). The struggles attract still other males, so that one female may become the center of a struggling mass. One such group which Banta caught had six males fastened together about a single female and five others nearby but not yet attached. The actual egg laying and fertilization of the eggs is accompanied by the formation of a close aggregation (72). In addition to the male that has been *in copulo* for some time these supernumerary males gather and, despite kicks from the first male, still manage to form a close clump. In *Rana fusca* one may find single pairs, but as a rule fertilization is a community matter. Supernumerary males also crawl over and among the egg masses and effect the fertilization of ova which may not have been reached by spermatozoa at the time of their discharge.

At the close of the breeding season, frogs scatter and resume a solitary, nonsocial existence.

c. Fish. Similar breeding clusters of fish have been described (159) with many identical details. With the rainbow darter smaller supernumerary males crowd about the spawning pair and appear also to shed spermatozoa. Reighard (160) has seen such behavior but in the main his studies (161, 162) emphasize the orderly spacing of breeding holdings in fish, a phase of the aggregation phenomenon with which the present report is not greatly concerned.

d. Snakes. Snakes are reported to form bunches in the breeding season similar to those described for frogs (53, 66, 174). Ellicott (66) records:

I first saw such a bunch of snakes on the stony banks of the Patapsco River, heaped together on a rock and between big stones. It was a warm and sunny location where a human being could scarcely disturb them. I reasoned that the warmth and the quiet of that secluded place had brought them together. Some hundreds could be counted, and all in a very lively state of humor, hissing at me with threatening glances and with such persistency that stones thrown at them could not stop them nor alter the position of a single animal. They would make the proper movements and the stone would roll off; all the snakes in this lump were common garter snakes (*Eutaenia sirtalis* L.).

The second time I noticed a ball of black snakes rolling slowly down a steep hillside on the bank of the

same river. Some of the snakes were of considerable length and thickness and, as I noticed clearly, kept together by procreative impulses.

e. Lunar periodicities. Such breeding aggregations are much more important in fresh water and land forms, with whom the surroundings are more injurious to shed sperm and eggs but they do occur among marine animals. With marine organisms the most spectacular expression of breeding aggregations is to be found in the case of the large number of animals whose breeding rhythms coincide to some extent with lunar periodicities. The literature on this subject (75, 83, 108, 112, 119, 121, 131, 143, 215) is extensive and while the facts are plain enough the fundamental causal relationships remain unknown. One illustration must suffice, based on the account given by Just for the swarming of the sea worm *Nereis limbata* in the waters around Woods Hole (112).

Nereis limbata has its swarming period only after twilight. Each run begins near the time of the full moon, increases to a maximum during successive nights and sinks to a low point about the time of the third quarter, again rising and falling to extinction shortly after the new moon. They appear in four periods or cycles during the summer, corresponding to the lunar cycles in the months of June, July, August and September.

Only fully mature animals swarm. The swarming begins shortly after twilight and lasts only for an hour or so. The swarming animals are attracted by the light of a lantern. Males appear first, darting through the water in curved paths in and out of the circle of the light. Females are fewer in number and swim more slowly. The males outnumber the females hundreds to dozens. In the next few minutes the numbers increase, waning again after about three quarters of an hour.

New females appear each night, but some males may presumably reappear on several successive nights. A swarming female is soon surrounded by several males. These swim rapidly in narrow circles about her. In a little while they begin to shed sperm, probably in reaction to some secretion from the female, rendering the water milky. Soon the female begins to shed her eggs, shrinking in bulk as she does so, until, a shadow of her former self, she sinks through the water to die.

2. *Hibernation*

Overwintering aggregations of animals have long been known. This phenomenon with social bees has been noted in scientific literature for almost two centuries (158). Barkow (13) in his monograph on hibernation written over three-quarters of a century ago has a short chapter in which he calls attention to the winter aggregations of lepidopterous larvae, adult ants, bees, true bugs, beetles, including the frequently observed case of the coccinellid beetles, carp and eel-like *Muraena angulla*, snakes, frogs, and a few mammals, including marmots and bats. Barkow advances no theory to account for the congregation of these animals, but states that there is a suggestion current that the animals aggregate as a result of response to their sense of smell.

This list of overwintering aggregations has since been much extended, especially by Holmquist (98, 99), who has made extensive studies on hibernating arthropods in the Chicago region. He reports that of 329 identified species taken during the winter season nearly 17 per cent were more or less closely aggregated. Omitting those known to be of somewhat social habits at other times of the year, about nine per cent of the species ordinarily solitary in the summer were aggregated in winter.

In the social bees careful experiments have shown that temperature control results from such clusters (153, 154) and Holmquist has unpublished data showing that other benefits may accrue from the cluster formation of hibernating ants.

In many cases these overwintering groups are essentially shelter aggregations apparently due to the small amount of serviceable shelter available. Often, however, not all the apparently equally desirable space is occupied, so that the aggregation cannot be entirely explained on the basis of unavoidable crowding. In other cases Holmquist has been unable to find any environmental differences to account for the location of the hibernating aggregation. These groupings are partially under temperature control, but as with other phenomena connected with hibernation, the temperature control is incomplete and the problem of the exact nature of the causal factors remains open.

3. *Aestivation*

Aestivating aggregations have been less studied. Land isopods will form aestivating groups which may be either homotypic or heterotypic. They have been reported to collect in large numbers in protected places and so pass the long, hot, dry summer of southern California (1).

4. *Moisture control*

The chief controls of the aestivation reaction of these isopods are temperature and moisture. Of the two, laboratory experiments show the latter to be more important (7). When land isopods of various species are placed on air-dry filter paper they collect in bunches within a few minutes unless the substratum is too dry. In this case they will run about actively until at the point of death. If the substratum be moist, the same isopods will remain quietly scattered. A somewhat similar effect of drought in nature is reported for the California quail (68). In an unusually dry season these quail do not breed but remain in flocks during the entire summer. The opposite type of moisture control is also observable. Too much moisture may induce well defined aggregations. Thus *Solenopsis geminata* (202), a species of ant which often nests in lowlands will, if the nest is flooded, aggregate in a ball of some 15 to 25 cm. in diameter with the larvae and pupae inside. By constant rotation they avoid too long submergence and at length may come against some solid object and so escape from the water. Wheeler (205) cites this case and mentions similar instances in this and other species of ants.

The formation of the dancing bunches of midges that one frequently sees aggregated in the space of a half bushel basket appear to be in part conditioned by the atmospheric humidity, although the absence of wind is another obvious prerequisite.

In both these cases the environmental conditions are uniform and the animals in grouping together react to each other only. There are also the place aggregations controlled by moisture when animals will collect in a limited area because it provides an oasis of moisture in an otherwise overdry environment. Thus land isopods can be made to collect at will in a given spot by making it moist. Selous (178) gives a striking picture of the congregating of large ungulates about an African drinking hole in the dry season. The common fruit fly, *Drosophila*, shows a somewhat intermediate condition when, struggling to escape too great moisture, it aggregates in shifting masses at the top of a projection; these masses continually fall apart and re-form as the flies move up again. When transferred to a dry bottle they resume normal behavior and spread over all the interior surfaces.

5. *Lack of normal environment*

The snake starfish, *Ophioderma*, lives in eel grass in certain locations along our eastern coast. Repeated efforts in summer months have failed to reveal this animal in contact with others of its kind in nature. They are often found near together but never aggregated.

Ten of these starfish were introduced into a laboratory aquarium made to approach normal living conditions by the introduction of eel grass. Nineteen hours later seven of the ten animals were sighted after a search lasting half an hour. One was found on the bottom at the side away from the strongest light; six were in the densest part of the vegetation in the same region, and although not in immediate contact, all of them could probably have been enclosed in a five-inch cube. The exact location of the other three could not be observed without disturbing them. Animals in the field are probably also close together without actually touching. Only such loose collections were ever seen in this eel grass aquarium. Extended experience with these animals in the laboratory leads me to conclude that the tendency to bunch is greatly reduced in proportion as favorable natural conditions are approximated, and that the animals so congregated are usually found in regions to which they have been directed by their tropistic reactions.

When, however, *Ophioderma* are placed as they are collected in a glass or similar container, they form dense mats of bunched animals with arms closely interwoven. The aggregations form in the shadiest part of the dish and are to be explained in part by the fact that the lower animals are shaded by the upper ones and so, having satisfied a negative phototropism and a positive thigmotropism, they remain quiet.

When these starfish are isolated and left for a week or more in separate dishes exposed to light frequently the arms are moved into contact until they present a sort of self-bunching.

Laboratory aggregations occur in a large number of animals. May-fly nymphs, various isopods, earthworms, frogs, etc., may readily be observed to form such bunches. The reaction appears similar to that which causes the collection of foreigners into communities in our large cities; that is, a group of similar animals tend to minimize for each other the disturbing effects of unusual surroundings.

6. *Sleep*

Fabre (69) found some hundreds of *Ammophila (Sphex) hirsuta* assembled under the shelter of a stone on the mountain side and speculated much concerning this gregarious condition of a solitary wasp. The Raus (156) found three related species sleeping in such assemblies, from which it would seem probable that Fabre was observing a slumber aggregation. With *Chalybion caeruleum* both males and females may be found aggregated at night in about equal proportions. As many as a thousand have been found in one colony. Marked individuals will return to the same sleeping place for at least two weeks. No one knows how the male of the species passes the day; the female labors about the nest in the daytime.

The solitary *Sphex* wasps appear to choose their sleeping quarters independently, but since they select the same sort of place, they tend to form spaced aggregations. *Prionyx* sleeps sometimes singly, sometimes gregariously, crowded close together on the top of a weed with equal numbers of males and females present but without observed copulation. The males and females of the horse fly, *Tabanus sulcifrons*, are reported also to collect

(90) in favorable places to sleep. Similar observations are on record for various other insects.

There is no evident protection from enemies in such assemblies. The sleep may be sound and extend so late that early birds could pick off the sleeping insects in numbers, as beetles are reported to kill sleeping butterflies (73).

The congregation of birds for sleeping has been widely observed (14, 25, 44, 208) particularly for martins, robins, grackles and crows. Many other birds are reported to gather in the roosts dominated by martins and robins. It is well known that bats also gather into sleeping aggregations (8, 82, 102). They may congregate in clusters comprising only a few individuals, or hundreds may hang with bodies touching. Some cluster so only in the daytime, others only at night. The groups may be homotypic or heterotypic. To the human senses these bird and bat roosts are easily detected by their odor, and perhaps that is a factor in guiding the bats to the sleeping place.

Allen (8) has banded clusters of these bats. He records recovering three of a group of four from the same place where they were banded after an interval of three years.

These sleeping aggregations appear to be without mating significance. The Raus did not see copulation among the insects they observed; in fact, in many cases, the sleeping groups were composed of males only. The robin roosts may contain both sexes and all ages of birds above the nestlings. With crows the common roost ends with the beginning of the breeding season, except for the bachelors, and in general these roosts are not occupied by the breeding birds. After the breeding season the birds may return in family groups, a situation to be discussed later at more length. In the bats the sexes are segregated (102) during the time of gestation and of the care of the young.

IV. HOMOTYPIC VS. HETEROTYPIC AGGREGATIONS

Heterotypic aggregations are those which are composed of more than one species; they appear to be of common and widely distributed occurrence. Unusual and dramatic combinations are frequently recorded, as that of fox and caribou (52, 190), fox and mountain sheep (182), predaceous and non-predaceous insects overwintering in the same restricted hibernaculum (98) and mixed herds of the large African animals, to which reference has already been made (178). The phenomenon of mixed flocks is well known among birds. The most extraordinary that has come to my attention is that recorded by Beebe (15) who observed a flock of 28 birds composed of 23 different species. Such heterotypic aggregations closely approach the associations of the ecologists.

The interesting problems with heterotypic aggregations concern the relative ease with which they may be formed and the degree to which they may become integrated as compared to homotypic groups. Land isopods form such groups and preliminary studies have not shown essential differences so far as physiological effects are concerned. There is evidence with the isopods, however, that heterotypic groupings occur more slowly than do the homotypic ones. Young spiders of the genus *Epeira* will mingle if family groups are intermixed (46), forming associations which are apparently as firm as if composed of but one family group; but different species of the same genus will separate out peaceably into distinct groups even if well mixed. In ants, of course, the antagonism may be much stronger; but

the situation in such social animals does not come within the scope of this review.

V. RESULTS OF AGGREGATIONS

After all we are less concerned about the methods of formation of aggregations and the factors conditioning them than we are with the physiological effects which such aggregations produce upon the individuals of which they are composed. The type and extent of such effect makes one of the crucial tests of the importance of the phenomena. If these aggregations are merely forced reactions resulting from limited space or from blind tropistic behavior or if they result only as an expression of a social instinct, their significance is much less than if they can be shown to have group value. Failure to observe such values for many aggregations led Deegener to conclude that their formation must be due to some inexplicable instinct.

In other words, in the investigation of this problem we must first inquire whether or not the aggregations have survival value. If such be found in a number of cases the problem is by no means solved, but the methods to be used in its solution will be more clearly indicated.

A. Harmful effects of aggregation

From the older, grosser point of view dominated by the idea of a struggle for existence between animals such aggregations are more obviously harmful than helpful, at least until they become sufficiently integrated so that members may be warned of the approach of danger by the multiplicity of eyes in the group, or can attack or defend more advantageously as a group than as single individuals.

An aggregation of *Dermestes* beetles feeding on a limited amount of carrion exhaust their food sooner when the group is larger. This aspect holds true whether we are concerned with leaf-eating caterpillars, sap-sucking aphids, or tissue-filling parasites. It is only with predators catching lively creatures as food that the feeding aggregation becomes of value. A school of young catfish is much more likely to catch a given *Daphnia* than is a single individual, and each member of the group is more likely to feed upon the *Daphnia* stirred up than if he swam alone.

The same number of individuals are obviously more easily gobbled up by an enemy when aggregated than when scattered. One of the sleeping clubs of bees or wasps described by the Raus would provide a substantial breakfast for the proverbial early bird, and a hungry centipede would have easy picking in a group of aestivating land isopods. Similarly a bunch of starfish in a limited amount of water exhaust the available oxygen more rapidly than would a single individual.

1. Deleterious effects of crowding

Jabez Hogg (92) apologized to the London Microscopical Society in 1854 for taking up their time with some observations on the pond snail "*Limneus stagnalis*" which had already been the subject of microscopical examination by such masters as Swammerdam and Réaumur. Then in the midst of his other painstaking observations he records that a snail kept in "a small narrow cell will grow only to such a size as will enable it to move freely" and this is the first recorded observation of the limiting effect of volume on growth.

Twenty years later Semper (179, 180) extended this observation to include the dwarfing effects of the presence of several animals in a limited space as compared with a single individual in the same amount of space as that occupied by the whole group. The whole literature on this point is much too extensive to review

or even to list here. Colton (37) writing about twenty years ago gives a good summary of the early literature and adds his own confirming evidence.

The dwarfing effect of crowding has been widely observed in the animal kingdom and has been found to affect both growth and reproduction. Recently Bilski (16) studied populations of tadpoles and derived a fairly simple mathematical formula to describe the influence of the density of animals upon the rate of growth. Pearl (145) and his associates have found that a similar equation describes the effect of density in cultures of *Drosophila* upon the rate of reproduction. Pearl points out that both equations closely resemble that of Farr for describing the relation between death rate and the population density in human communities.

A large number of suggestions have been put forward to account for these crowding effects. Hogg in 1854 said naïvely enough that the animals adapt themselves to the necessities of their existence. Semper, twenty years later, unsatisfied with this statement but unable to find any specific causal agency, postulated the presence of some unknown substance necessary for growth as oil is for machinery. This material he thought must be absorbed in a definite quantity if growth is to be normal. Since the substance was supposed to be present in minute amounts, the greater the crowding in a given volume, the less the growth. Pearl writing only last year concerning the decreased egg laying in the crowded chickens could not be much more definite. He postulates an unexplored physiological disturbance which "in our ignorance we must call psychological."

Fortunately some progress has been made with water animals towards finding the causes of this physiological disturbance. Semper cites the obvious limitation of food as one cause. Yung (218, 219) found that lack of oxygen causes dwarfing of tadpoles. Vernon (201) concluded that the echinoderm larvae he studied in restricted volume were stunted by the increased concentration of excretory products. These observations have been widely extended. The limiting effect of excretion is particularly marked in ciliate infusions (84, 212, 214). Recently Goetsch (81) has introduced a clever experimental method which allows him to separate the factors of available space from available volume. He introduces into his experimental aquaria, tubes thrust through corks to keep them afloat. The lower end of the tube is covered by gauze, which allows diffusion connection with the whole aquarium but limits the amount of available space. By equalized feeding another obvious factor is controlled.

Goetsch experimented upon sessile hydra, slowly moving planaria, and amphibian larvae which are capable of rapid locomotion. As might be expected he finds different factors important for different animals. Thus with hydra, volume per animal is the controlling factor because of the restriction of food which it conditions. There is no stimulation or depression caused by the crowding of hydra in a narrow space and within reasonable limits concentration of excretory products is not effective. With planaria food is again the most important factor but growth is markedly inhibited by the concentration of excretion products or of stale food. With the active amphibian larvae, if food is controlled, the major limiting factor is furnished by the more frequent collisions in a dense population or in restricted area with the concentration of excretory products playing a wholly secondary rôle.

Drzewina and Bohn, in connection with their studies on the relation existing between mass of toxic liquids and the contained mass of animals have found many cases of protection furnished by increasing the numbers of animals present in the same

amount of solution. These will be reported later. In some instances they record the opposite results (58, 59).

When KCl was used as a toxic agent with cultures of *Convoluta*, a small marine planarian, other things being equal those in the solution containing the larger number died first. Similar relations hold when the same number of individuals are placed in differing amounts of the same strength of KCl solution. Those in the smaller amount of liquid die more rapidly. The freshwater planarian, *Polycelis nigra*, reacts similarly. These investigators believe that the planarians give off a substance which causes auto-destruction, and obviously, if this be true, such destruction is hastened by increasing the mass of individuals in proportion to the amount of liquid.

Their interpretation is supported by the observation that if two fresh planaria are introduced into a solution of KCl which has already contained others, their death is hastened, but if, after an hour in such solution one removes them to a new solution of similar strength, their death is again retarded. Before accepting this hypothesis it would be desirable to inquire into the oxygen tension and respiratory exchange under the various conditions. Some of the relations outlined are those which one would expect from decreased oxygen tension.

As these selected observations show, it is easy to demonstrate harmful effects from crowding of paramecia or of men. This makes the attempt to locate a positive survival value of relatively unintegrated aggregations, which the widespread occurrence of the bunching habit would lead one to expect, at once more difficult and more important.

B. *Beneficial effects of aggregation*

In the case of breeding aggregations and of young associated with and watched over by the parents, or of groups protected by sentinels, the gregarious habit has obvious advantages. More refined laboratory observations have revealed unsuspected benefits that may result from aggregations even in a very low state of group integration.

1. *Maintenance of water content*

Aggregations of land isopods will take up water less rapidly from an over-moist environment (7) than will their isolated fellows, and conversely, they will also lose water more slowly under dry conditions. The formation of bunches helps make these isopods more independent of the water content of their surroundings and markedly decreases the rate of change of body moisture when this is out of equilibrium with their environment. In this way the length of life may be increased especially when the animals are exposed to a drying environment to which they are particularly susceptible. In one experiment ten grouped isopods on a dry background of filter paper were all alive and active after 7.5 hours, when six entirely similar animals isolated under similar conditions were all dead from loss of water. Such relations are known to hold for earthworms. Shelford (184) found that a ground beetle, *Pterostichus adoyus*, may react to a gradient of different rates of evaporation either by coming to rest in the moister region or by aggregating in the driest part. The phenomenon is probably of widespread and general significance.

2. *Tonus maintenance*

Respiration studies on the effect of aggregation on land isopods have shown that bunched animals are respiring at a more rapid rate after the animals have stood for some time. Since the experiment was carried on in the absence of food, the rate of respiration decreased markedly in

both isolated and aggregated individuals but under the conditions tested this reduction takes place approximately twice as rapidly with isolated as with bunched isopods.

Studies of the total amount of oxygen consumed during such a starvation period by isolated and bunched starfishes (*Ophioderma*) show that the bunched individuals consume more oxygen over such a period than do the isolated individuals. Mr. M. W. Eddy, working at my suggestion, has found that aggregated young catfish (*Ameiurus*) have a higher rate of respiration than do artificially or self isolated ones of the same age. Preliminary determinations on a number of other animals indicate that such conditions are widespread when the animals are tested under conditions approaching those obtaining in nature.

3. Heat conservation and regulation

It is difficult to hold to the intention of avoiding discussion of aggregations among the social animals. The matter of heat conservation by aggregating is best illustrated by the example of the honey-bees. These poikilothermal animals show some ability in regulating their temperature as individuals (155) but still more in the winter clusters (79, 153, 154). When a bee colony is without brood, if the bees do not fly and are not disturbed they generate practically no heat until the coolest point among the bees reaches a temperature of 14 deg. C. At higher temperatures the bees remain scattered over the comb. When this critical temperature is reached they form a winter cluster and begin to generate heat.

The temperatures within the cluster do not remain constant and are affected by the length of confinement and by the presence of brood, both of which cause an increase in temperature. Heat for warming the colony is produced by muscular activity within the cluster. The same fanning movements that serve to cool the hive in summer also serve, with other muscular activity, to warm the winter cluster. In winter the bees also retain water in their bodies and so avoid the loss of heat that would be necessary to evaporate it (144). Steiner (196) has described similar relations for one of the ants. He emphasizes this matter of warmth as an important factor in the development of social life in animals and maintains that animals cannot co-operate well unless they are able to remain warm over long periods of time.

4. Protection from various adverse conditions

The common brittle starfish at Woods Hole, *Ophioderma brevispina*, if isolated into glass dishes of sea water will undergo fragmentation of the arms much more rapidly than occurs when a group of ten or so are placed under wholly similar conditions. The group immediately forms a close aggregation which for some reason inhibits the animals from self-mutilation. In one case the ratio of broken arms was nearly twice as high in isolated individuals as with those grouped. Evidently the self-bunching which is frequently practised by solitary animals has not the protective value of group bunching.

a. Relation of mass of animals

Drzewina and Bohn (55) became interested in the possible protection from toxic substances furnished by a mass of animals as compared with that of a single individual exposed to the same intensity of the toxic agent. They recognized that added immunity due to some sort of group protection might explain the fact that many animals live near together in nature. Thus *Convoluta*, the tiny, green flatworm common on the coasts of Brittany, is

found in loose groups in the sands of tidal flats where they are exposed to marked dilution of the sea water by rains, particularly if the rains come at low tide. Experiments showed that these worms can resist dilution of the sea water much better when they are present in large numbers than when there are but few present.

Similarly, if placed in dilute suspensions of colloidal silver, *Convoluta* in small numbers die in about four hours, while with twenty-five to fifty times the number of worms in the same amount of the same strength of silver suspension, death occurs in about forty-eight hours. Similar relations hold over a wide range of dosage. Schuett (176) has verified this general situation, using *Planaria dorotocephala* in this laboratory.

Similar results were obtained with infusorians such as *Stylonichia*, *Paramecium*, *Colpoda*, *Vorticella*, and *Stentor* (57). In suspensions of colloidal silver of from one to five drops per cc. the resistance of tens was compared with that of hundreds or thousands. Always, when a minimum amount of the parent culture solution was introduced, the isolated individuals were much less resistant.

Drzewina and Bohn obtained similar results with tadpoles of the brown frog, *Rana fusca*, and even when different concentrations of spermatozoa of sea urchins (*Strongylocentrotus*) were treated with different toxic agents (60, 61). The sperm retained fertilizing power longer when the concentration was greater. Hinrichs (91) has found that the rate of loss of fertilizing power by spermatozoa of *Arbacia* treated with ultra violet radiation is directly proportional to the dilution.

Supporting evidence from a separate source comes from the observations of Robertson (165) upon the Australian infusorian, *Enchelys farcimen*. A temperature of 30 deg. C. prevents subcultures of this protozoan from multiplying and the isolated individual almost always dies. But shade temperatures of 30 deg. C. are known in South Australia where wild *Enchelys* live. Isolated wild infusorians brought into the laboratory gave the same reaction, but if the culture slides were populated by twenty to thirty individuals they could successfully resist exposure to temperatures of 33–34 deg. C. for as long as seven days in succession without apparent injury or abnormality. A similar number of individuals put into fresh hay infusion at this temperature survives and multiplies while isolated individuals inevitably perish.

b. Relation of volume of liquid

The converse experiment is made by keeping the number of animals constant and varying the mass of the liquid. Such experiments were performed by Drzewina and Bohn (57) with results which support their conclusions reported above. Experiments with infusorians and with a small leech, *Glossiphonia bioculata*, strongly indicate that with the solutions used the dilution of the toxic substance is less important than is the mass of the liquid environment.

The same problem in less severe form is to be met in isolation cultures of microorganisms and of tissue cells. Wildiers (210) found a relation between volume and the success of his cultures of yeast, with cultures growing better in the smaller volumes. Kuster (115) records that the isolation of a single organism in too large a volume of culture media results in death or in great delay in multiplication. Barber and associates (204) could not obtain growth from a single tubercle bacillus or an anthrax spore introduced into a guinea pig or a mouse; several must be introduced before they thrive.

Jennings (110) summarizes the experi-

ence of workers with isolated paramecia when he states that

> long continued cultivation on slides does produce a depressed condition. There are some stocks that will not stand it at all, though they live perfectly in mass culture.

It is also true when the same culture medium is used with both, that the stocks cultivated in isolated condition frequently die out while the same stock will live in mass culture.

Peters (152) lays stress on the relation between the volume of the medium and the number of colpidia growing in it at early stages in the isolation. Many attempts were made to get individuals to grow in small test tubes with about one cc. of culture fluid, but all were failures. He suggests that in order for growth to proceed, the organism has to modify its environment, probably by adding some synthesized substance in sufficient concentration for growth. When a sterile subculture containing 20 to 40 organisms has been obtained the subsequent subcultures are easily made.

Robertson (169) reports similar experiences with *Enchelys*. In his cultures, single infusoria isolated in volumes exceeding 1 cc. rarely survive and those in more than 0.1 cc. frequently fail to divide.

The tissue-culture workers have also contributed some evidence on this point. Testimony is unanimous that isolated single tissue cells do not multiply. Rous and Jones (172) were impressed, as several had been before them (173, 211), with the striking tendency to reunite that is shown by isolated tissue cells, but they did not see division or multiplication of such cells. Burrows and associates (31) state that isolated tissue cells planted in plasma may show movement but they do not grow. They find that growth takes place only about fragments of tissue, and that if the transplant is not too large, growth *in vitro* is directly proportional to the size of the fragment.

Fischer (71) found no evidence of cell division among isolated cells although he studied hundreds of such isolated fibroblasts. When ordinary tissue cultures were cut in two and transferred to a new medium the cells grew more rapidly at the center than at the periphery. If the periphery of a mass of such cells growing *in vitro* is isolated from the main body by an incision the peripheral cells no longer grow, on reincubation, although the densest part of the main cluster grows rapidly nearby.

Gemmil (80) a quarter of a century ago reported that dilution shortens the period of vitality of spermatozoa. Lillie (120) gives directions for a practically quantitative experiment testing the effect of dilution on the sperm of *Arbacia*. Extremely dilute sperm suspensions (1–240,000 per cent) lose the fertilizing power in about six minutes, while a concentrated suspension of one per cent may retain this power for more than two days.

c. *Explanation of mass relations*

Drzewina and Bohn present evidence that the greater immunity of the larger group is not due to the using up of the active toxic substance more rapidly by the larger number of animals. A number of infusoria in a suspension of colloidal silver of the same volume but five times the strength of another suspension will remain alive after isolated animals in the weaker suspension are cytolyzed. The relative color of the two show that more silver is still present in the medium containing the group.

The following procedure gives further evidence that the greater immunity furnished by the group is not due to the exhaustion of the toxic agent (57): Decant

off the silver colloid suspension in which fifty larvae of *Rana fusca* have stood for twenty-four hours. The color will show that silver is still present. Now add the same number of drops of silver colloid originally used and introduce two new tadpoles. As a control place two similar tadpoles in a fresh suspension of the original strength. Drzewina and Bohn report that the latter die, as is the rule for isolated tadpoles, while the former, isolated into a stronger suspension in which tadpoles have lived for a day, will survive.

From such observations they conclude that when attacked by toxic agents, animals give off rapidly a substance or substances which are protective. If the individuals are present in sufficient numbers in proportion to the volume of the reagent, the defense may be effective; if isolated it is much more likely to be ineffective. Evidently a reserve of this hypothetical protective substance is accumulated (56) until it will protect isolated individuals introduced into a decanted and reinforced solution. Less protection is furnished by water in which worms have stood, but which lacked the toxic agent, and when the colloidal suspension is diluted the protection is greatly weakened. Drzewina and Bohn have examined the nature of this protective substance and report that it appears to be specific, but the experience of this laboratory (176) has been that under controlled conditions planarians are protected from the action of colloidal silver by the presence of numbers of carefully washed individuals of *Dendrocoelum*, *Daphnia*, *Asellus*, pond snails, pond leeches, and even by pond mosses. This protection has been reciprocal whenever tested. In our experience the protective secretion appears to be the slime which many of these organisms produce in large amount and which adsorbs the toxic silver particles. Our experience in this matter resembles that of Bresslau (24) rather than that of Drzewina and Bohn.

Burrows and Suzuki (32) think that disintegrating tissue-culture cells supply nutrients necessary for growth. Fischer (71) concludes that beside the growth-promoting factors found in the tissue juices, there may possibly be something produced in the body of the cell or of certain cells only, that initiates cell division and is carried directly from one living cell to another.

Robertson infers that some necessary substance passes from the infusoria into the medium. If the amount of the medium is too great reproduction and even maintenance become impossible. He suggests that the death of isolated infusoria at high temperatures is due to the excessive loss of this substance from the nucleus on account of the increased permeability of the nuclear membrane. The group is able to protect itself because the concentration of this hypothetical substance is supposed to come to equilibrium before the individuals of the group have lost an excessive amount.

Suggestions similar to these have been made (80, 91, 120) to account for the rapid loss of fertilization power by dilute suspensions of spermatozoa.

5. *The lag phenomenon*

When a single cell is isolated into a new culture medium a longer or shorter latent period usually follows before reproduction begins. This is known as the lag period. It has been much studied in bacterial cultures (147), in *in vitro* cultures of vertebrate tissue and in protozoan cultures (165, 169). The duration of the lag period depends in part on the condition of the parent culture. If this is reproducing at maximum rate and if the nutrient medium is taken from that of the original culture, frequently no lag ensues (147).

With some media even under these conditions the lag phenomenon persists. Robertson (169) finds that, other things being equal, with infusorians the lag may be shortened by making a gradual transfer from the parent culture to the new subculture.

This lag phenomenon is of interest in our problem because of the indication it gives that organisms isolated into new conditions are markedly affected by the change and because of observations (147) that if the inoculum be small further diminution of the seeding lengthens the lag period; the smaller the seeding the more marked the lengthening.

Robertson's explanation of the phenomenon, although expressed in terms of his hypothesis of an autocatalytic agent, is in general similar to the older idea of Penfield's for bacterial cultures. Penfield proposes to explain the lag by assuming that some substance "*c*" may be required which is produced not from "*a*" already in the solution but from "*b*" which must be produced by the organism from "*a*."

6. *Robertson's allelocatalytic effect*

Robertson (171) found that when two infusorians (*Enchelys*, *Paramecium* or *Colpidium*) are freed from parent culture media by washing, and are introduced into some restricted volume of fresh culture medium, the early rate of reproduction after the lag period is not merely double that of a single infusorian of the same species similarly treated, but reaches some multiple in excess of this. He reports that he has obtained a rate of from 2.5 to 10 times that which might have been expected. This increased rate of reproduction, which Robertson calls the allelocatalytic effect, he attributes to the diffusion of some agent from the organisms into the culture medium, by which their reproduction rate is accelerated.

Fischer's work, mentioned above, in which he found that fibroblasts grow only when tissue cells are numerous and close together, can be interpreted as giving supporting evidence to the allelocatalytic hypothesis. Burrows (30), growing cancer cells *in vitro*, found a similar stimulation.

On the other hand Cutler and Crump (41) with cultures of *Colpidium*, failed to find the allelocatalytic effect if the volume of the medium is reduced, and Greenleaf (84) records his failure to confirm Robertson's work, using *Paramecium* and *Pleurotricha*. Peskett (148, 149) observed such stimulation to division in only three cultures of yeast out of 128 examined, and later in extended observations failed to find evidence of Robertson's allelocatalysis.

Robertson (170, 171) has reexamined the problem in the light of these results and explains the failure of other workers as being principally due to lack of washing the organisms before transfer. He reports the allelocatalysis increases with progressive removal of preformed catalyst until a maximal effect is reached just before its total removal. He also emphasizes an earlier statement that in comparing the reproductive rate, care must be taken to estimate the population some time before it has attained maximum density. The end result of introducing a second individual is to reduce the rate of reproduction, since the final maximum is the same in all cases and is independent of the size of the seeding.

Peskett returns to the problem in his 1925 papers (150, 151), apparently using very careful technique, washing his transplants and plotting a growth curve based on a number of examinations at different phases of the culture, but again fails to find evidence for the allelocatalytic effect.

Cutler and Crump (42) also repeated

their experiments with *Colpidium*, thoroughly washing their animals before transfer. They again failed to obtain evidence of the stimulation demanded by Robertson's hypothesis. It may be that their technique differs from Robertson's sufficiently to account for some difference in results, since the infusorians which Robertson washed were frequently injured in the process, while Cutler and Crump found no deleterious effect from their washings; or there may be a difference inherent in the stocks used.

Here the matter of allelocatalysis, of obvious interest to any student of animal aggregations, rests at the present time in a sufficiently muddled condition to merit the experimental attention it is receiving at this and doubtless other laboratories.

7. *Other evidence*

On the other hand there is a mass of evidence that organisms do produce substances capable of causing growth stimulation. The existence of vitamines (62), the discovery that organic substances extracted from bacterized peat markedly stimulate plant growth (20–23) and that preparations from a variety of living tissues yield an extract that stimulates the growth of yeast (64, 65, 77) all indicate that organisms may give off substances into the surrounding medium which might markedly affect other animals nearby.

The possibility of a more subtle effect is indicated by the work of Gurwitsch and his associates (85–87, 157), who report that they can stimulate the number of mitoses by bringing the tip of one growing onion root in close contact with another but at right angles. The effect seems to be propagated in a straight line as a pencil of radiation, which tests indicate has a wave length of about 2000 Angstrom units. They report similar results with macerated living onion tissues, but narcotized tissues fail to be effective. They even find evidence of marked heterotypic stimulation with *Helianthus* roots acting on onion, and whole or macerated rapidly growing tissue of tadpoles is said to cause some stimulation of mitoses when given an opportunity properly to radiate growing onion root tips. Obviously such effects need verification before their implications are discussed seriously.

Taken as a whole, the evidence collected independently by a number of workers upon a wide range of organisms indicates that in many cases the group mav possess valid survival values. These may be much more refined than the more obvious advantages postulated by the earlier view of the struggle for existence and may easily be concealed by gross experimental methods. In fact, the obvious advantages may be lacking and still the aggregation can show survival value. Such advantages as do exist are not universal either among different kinds of organisms or with the same individuals in different environments; but the fact that they may exist even in groups brought together artificially by a laboratory experimenter indicates that they deserve serious consideration from the student of social origins.

8. *Influence of aggregations on sex*

There is another growing lot of evidence that aggregations of animals may exert a profound influence upon each other to be found in the effect of such groupings upon so fundamental a characteristic of animals as their sex. Over ten years ago Baltzer (10) found that if the young, free swimming, sexually indifferent larva of the marine worm *Bonellia* attaches itself to a female of the same species it receives a sex determining substance from the host and becomes a male. If, on the other hand, it

develops solitarily, it becomes a female. In this case organic attachment is concerned, a situation which we are not discussing seriously in this paper.

The conditions are different in the boat-shell snail, *Crepidula plana*, which is common on our New England coast. These too are protandric hermaphrodites. They live sedentary lives on the shells occupied by hermit crabs. Gould (82a) found that the development of the male phase depends on the nearby presence of a larger individual of the same species. Such an individual is frequently a female but that is not necessary, for a larger male will have the same influence. Some sort of stimulus passes from one to the other but Gould was not able to discover the nature of this stimulus. When a male becomes removed from the neighborhood of a larger *Crepidula*, the male organs degenerate and after a period of sexual inactivity, female sexual organs develop.

The relations between aggregating individuals and sex are just as interesting in the water fleas commonly called *Cladocera*. These animals reproduce parthenogenetically for a longer or shorter period during which the population is wholly female. Such a period is followed typically by an epidemic of bisexuality, the exact causes of which have long been a challenge to experimental zoologists.

Banta and Brown (12) have recently found that a crowding of the mothers will cause the production of a variable number of males, while females of the same brood, given identical treatment but uncrowded, produce only females. Dr. Agar has told me personally that he has confirmed this observation "to the hilt." Banta and Brown suggest that the appearance of the males in a crowded culture is due to an excess accumulation of excretory products, since they find that a number of depressing conditions such as lowered temperature, increased carbon dioxide tension or the introduction of uric acid has the same effect, particularly in crowded dishes. They think that the metabolism of the mothers is reduced by the effects of the crowding and that such reduced metabolic rate during the maturation of the eggs favors the production of males.

VI. AGGREGATION INTEGRATION

Animals living in a given habitat can be shown to be more or less closely interrelated. Darwin's famous demonstration in logic, proving a relation between the number of maiden ladies and the yield of clover seed in the English rural districts, is an illustration of this fact. Ecologists have attempted to systematize this "web of life" under the name of "biotic communities" or "associations" and have made it the basis for the modern development of ecology. Bodies of fresh water furnish the most complete illustration of this point of view, as was clearly pointed out by Forbes (74) almost forty years ago. In his essay on the "Lake as a Microcosm" Forbes shows the intimate relationship between all inhabitants of a small lake, plants as well as animals. The microscopic protozoa are seen to be members of the loosely integrated community as truly as the black bass, which are at the apex of the food series. Relationships concerned with food and space form the main integrating factors of such a microcosm, and these are sufficiently strong so that the whole may be recognized and treated as a unit. It is upon such units that modern ecology is built.

Obviously such a unit may be somewhat vaguely defined. As Mathews (130) says of the protein molecule, the unity of the animal association is to be compared with that of a village to which individuals may come, or whole families may be replaced,

or move away without replacement, and still the village retains its identity, not only in name, but by the retention of certain distinctive and more or less elusive attributes. Within this general organization of the village or of the animal community there may be all gradations from solitary to highly social individuals.

From the point of view that even so heterogenous a group as an ecological association may still be more or less closely integrated one is in much better position to study the different degrees of integration represented by the types of animal aggregations we are considering.

The first step toward social life in lower animals is the appearance of tolerance for other animals in a limited space (7) where they have collected as a result of random movements or of tropistic reactions to their environment. This may occur in connection with some phase of breeding activity but it may also be exhibited without sexual significance. Some of the less complex of these aggregations may exist because there is an absence of dissociating factors among a group of animals that have been hatched out in a restricted locality, or that have been brought together by any other process. Thus some of the aggregations resulting from tropistic responses may well owe whatever permanency they possess to the absence of disruptive factors rather than to any inherent gregarious tendency or possible advantage.

A first advance in social life is made when these groupings serve to promote the welfare of at least some of the individuals forming them, illustrated by the slower rate of moisture change in an aggregation of land isopods out of water equilibrium with the surroundings. Under conditions of drouth this results in a definite prolongation of life. Other examples are found in the preceding section.

The land isopods and *Ophiodermа* have gone little beyond such a stage in their social development. There is some slight evidence of mutual attraction, but the experiments to date do not indicate how much of this would also be exhibited toward similar inanimate objects. There is also slight evidence of integrated group behavior in that the bunch shows occasional periods of activity apparently originating in one individual and passed mechanically through the group. Such activity may be the beginning of disintegration of the group, but it frequently results in a closer aggregation because the animals may move closer together during their brief period of activity.

The state of development of integration by means of which the group acts as a unit, once it appears, is obviously a very important criterion of the degree of social development that has been attained. When there is no integrative action one is dealing with a crowd, a mere collection of individuals within a limited area. Apparently it was this aspect that Szymanski (197) had in mind in distinguishing between primary reactions, the reactions of the individual, and secondary reactions, the reactions of the individuals as members of a group. On the whole the state of development of group integration appears a better criterion than Deegener's (45) touchstone, social benefit, for attempting to evaluate the degree of social life existing within a group.

1. *Tactile integration*

The simplest form of group integration is furnished by animals in physical contact when they respond by group behavior to tactile stimuli transmitted directly. Such integration may reach a sufficient degree of organization for the group to show synchronous behavior. *Liobunum*, the harvestman, has been ob-

served by Newman (141) to give such reactions. When first seen they covered an area about five feet in diameter and were perfectly motionless. When the observer came close they began a rhythmic stationary dance practically in unison. This died down shortly but could be reinduced by further stimulation.

When the colony was first seen the long legs of neighboring individuals were interlocked, which would sufficiently account for the transmission of stimuli through the group. It should be noted, since we are interested in the state of integration of the aggregation, that the rhythm was not perfectly synchronous at the beginning but became practically so after a few seconds.

Such integration due to tactile transmission is highly developed in the sleeping groups of bats (8), which may hang in compact clusters, as already mentioned. If one be touched the whole cluster may drop. Allen caught eighteen by holding an insect net under the group and touching only one of the outer bats.

2. *Contact-odor integration*

Sex recognition, which frequently causes animals to give characteristic group reactions, often with only two animals, is frequently accomplished by contact reactions alone (9, 11, 35, 139, 146). Among other methods of sex recognition, that due to chemical senses deserves prominent mention. This is well illustrated by the long distances certain male moths will fly to cluster about a female ready to copulate. Animals may aggregate at other than the breeding season due to the same sort of stimuli, and this stimulus is also frequently effective in maintaining an aggregation once formed; witness the classical case of *Paramecium*. Such reactions are apparently widespread and may be one factor in the maintenance of schools of fish, because some fishes seem to be able to sense the difference in chemical concentration between the center and periphery of the school, a difference which, in its turn, the school itself maintains. Much of the social organization of the ants is built on a combination of these two senses, since ants apparently live largely in what to them is a world of contact-odor forms (205).

3. *Visual integration*

Sight plays an important rôle in the integration of animal groups. When one vulture soaring aloft sees another swoop miles away, he moves over and also swoops; his reactions are seen by others and thus these scavenger groups congregregate rapidly, although they practically lack a sense of smell.

Aggregations of male frogs in the breeding season will follow and frequently tightly clasp any moving object—salamander, fish, other males, etc.—a reaction based at least in part on sight. Other instances might be multiplied, but one spectacular one, that of the synchronous flashing of fireflies, must suffice.

A considerable controversy has been waged over this subject but the observation-experiments of Hess seem to have established the fact of its occurrence (89). He found a valley of fireflies flashing in unison, with the flash apparently initiated on a hill at one side, from which it spread almost instantaneously over the valley. The next night in the same place the observer was able to obtain at least partial control of the flash, and to alter to some extent the intervals between flashes. With a pocket flashlight he gave the initiating signal just before it would normally have occurred, and the insects followed the artificial lead until the interval was reduced to three-quarters of its original duration, and then one-half.

At the second trial at one-half the original period fewer insects followed the flashlight, and after that the unison was broken.

It seems probable here that we are dealing with a phenomenon of two distinct aspects (17). One is a recovery response similar to recovery from fatigue. Such flashing would rarely be synchronous or near-synchronous. On the other hand there appears to be a releasing stimulus which, in the cases observed by Hess, might come either from the pace-setting flash of a firefly or of an electric torch. This brings up the problem of the leader in group integrations, for which we have not space here. It is discussed at some length by Child (34).

4. Integration by sounds

Among many animals group integrations occur as the result of sound production. To be sure of this one must have evidence that behavior is altered as a result of sounds. The fact that collections of animals, such as frogs or insects, are producing sounds which are loud to the human ear is not good evidence that they have group significance (124). As reported earlier, there is evidence that among some animals sounds may be used in sex recognition. Perhaps they are more often of sexual significance in general sex stimulation, which, while of advantage to the group, may yield no advantage to the sound producer and may even result disastrously in the case of young deserted by a nesting bird who has been stimulated to renewed sexual activity by the outburst of song. Such cases have been observed by creditable ornithologists (186).

Ohaus (142) and Wheeler (207) report that the *Passalus* beetles, which have the habit of boring in logs, are kept together by stridulatory signals. Wheeler has more than once spoken of his observations indicating that aerial sounds may play a part in the integration of ant colonies, but on this point there are other observations to the contrary (70).

Beebe (15) thinks that there is a close correlation between habitat and habits of tropical birds and the development of their voice, which is popularly supposed to be one of the principal attributes of tropical birds. Solitary birds, living in the open country where sight is more or less uninterrupted, he reports to have a tendency to negligible voices. Inhabitants of dense jungle, if solitary, have remarkable vocal powers, with loud staccato calls or with insistent rhythm. Such birds may be nocturnal in habit. Birds living in pairs or in families have, for the most part, vocal organs which they use to good effect, but they lack the superlative voice development of solitary birds. Birds living in flocks have voices that are still less in evidence, though there are notable exceptions to this rule, as, for example, the parrakeets.

In the matter of vocal performance, as with tactile and visual integrations, group synchronisms have been reported. The group singing of the western meadowlark is an example among birds. One of the most interesting cases is that of the snowy tree cricket, which has been much studied, and which Fulton (78) reported to effect changes in chirping rate in order to chirp in unison.

Shull (188), a careful and critical observer, concluded earlier that real synchrony does exist in the chirping of this tree cricket. Later he concluded that cases of synchronism were usually accidental but he still believed that the singing insects do influence one another. Lutz (124) is skeptical both concerning the fact of synchronism and of its importance, at least in this case.

Synchronic behavior may of course merely mean that the group, while reacting as individuals, receive the stimulus at the same time and so react simultaneously. This is illustrated by the responses Minnich (138) obtained when he exposed aggregations of caterpillars to various sounds. Such synchronism has no bearing upon the problem of group integration.

Much emphasis has been placed on the rôle played by the human voice in the integration of human society; some social psychologists prefer to define man as a language animal. In this he does not appear to be unique except in the degree to which language has been developed in his species. Craig (39), in discussing voices of pigeons as a means of social control, finds that in animals with so highly developed instincts as birds, there is still much of the social life that cannot be explained on an instinctive basis. The reaction of the individual pigeon must be adjusted to meet the activities of other birds, its parents, its mate, its young, its neighbors and chance strangers. The adjustment is very delicate and requires that each individual must be susceptible to the influence of others, an adjustment which is largely accomplished by vocal means.

Lutz recently examined the importance of insect sounds and is inclined to question strongly their having any group value among these animals. Perhaps more time has been spent on the vocal-auditory method of group integration than is justified by the conditions obtaining at the aggregation level with which this report is immediately concerned. Its interest by reason of its importance with the higher animals must be the excuse.

It is profitless to speculate at present concerning the possibility of other, more subtle methods of group integration such as the observations of Gurwitsch suggest may result from exploration in the field of biophysics.

VII. SOCIAL SIGNIFICANCE OF AGGREGATIONS

So far we have seen something of the kinds and the extent of the aggregation phenomena in the animal kingdom and of the direct and indirect forces acting to control the formation of aggregations. We have outlined the present status of our knowledge concerning the physiological effect of aggregations and have found good evidence that some such groupings may have survival value. We have just seen that there exist methods of integration, not necessarily volitional, which may serve to organize a group closely; and that different degrees of integration exist in aggregations.

It has perhaps been implied without discussion that these aggregations have social significance. The question remains to be faced directly. This should lead to an extensive review of the evidence concerning the origin of the social habit, but instead we must limit the discussion by citing summaries of generally accepted points of view and testing these against a few of the known facts.

It is generally assumed at the present time that the gregarious or social habit in animals is at bottom an outgrowth of aggregations resulting from the association of young individuals with one or both parents. In special cases or at critical periods in social evolution, it is assumed that the period of the association becomes lengthened and the family comes to react as a unit under many conditions. Some such explanation for the origin of human society is current among sociologists, who derive organized society from the family by way of the clan (97, 117).

Students of social life in insects, especially as it exists among wasps, bees

and ants, usually adopt a similar explanation for the origin of the social habit (116, 128). Thus Wheeler in his studies on ants (205, 206) and more recently in his review of social life among insects (207) regards the insect colony as a result of the extension of the natural affiliation of mother and offspring. Wheeler's particular contribution is his theory that mutual feeding (trophallaxis) is the bond that unites parents and offspring in the social insects; the mother takes larval secretions in return for supplying food to the larvae. Wheeler also shows that the social habit has arisen *de novo* at least twenty-four different times among the insects alone, in nearly that number of natural taxonomic families or sub-families belonging to five different orders.

Opposed to this more usual view is that proposed by Herbert Spencer (192–195), which is that colony life arose from the consociation of adult individuals for cooperative purposes, as among wolves and various insects, which as we have seen, may collect under certain circumstances. From these instances Spencer suggests that in some cases permanent swarms arise and that natural selection will establish such of these groupings as are advantageous. In terms of human society, this view would stress the importance of the gang, rather than the family, as a preliminary step in the evolution of the social habit. It is important to note that the gang cuts across family lines in its formation. Unfortunately for Spencer's point, which may well be correct in some instances, he illustrated his theory by a concrete example among ants that probably owe their social development to an extension of the family.

Wheeler expresses the usual attitude toward these consociations when, after describing some instances of aggregation in ants, he dismisses them as either entirely fortuitous instances, which would occur wherever ants might be abundant and places of refuge scanty, or as the manifestation of highly developed social proclivities, and not of such proclivities in process of development.

It is worth emphasizing, as Child (34) recognized, that both the congregation and the family basis of societies are in fact but two different kinds of aggregations, so that, at all events, aggregations of some sort are essential for the development of the social habit. In other words, this phase of the problem of social origins is not whether the social habit as seen among insects, birds, man, etc., arose from such aggregations as we have been discussing in earlier sections, but whether they arose from a family aggregation or from one of another type. Deegener (45) recognized this division of aggregations, which does not seem to have been understood by many writers on the subject.

Discussion of the problems of the origin of the family must be reserved, but it is at least thinkable, and there is enough evidence to warrant further inquiry, that the human family (76, 103), and perhaps all sexual phenomena among animals as well, were conditioned in their development by the previous formation of aggregations, which primarily had no sexual significance, but possessed other survival value.

The other aspect of the problem is concerned with whether or not larger social organizations always rest on family units. Observations on bird behavior furnish interesting information on this point. Spencer's theory would require that the flock be formed by the coming together of individuals; the more accepted theory would emphasize the importance of the family. The question at hand is, which of these theories actually holds true in the seasonally recurring development of bird societies?

There is evidence that birds do migrate as families (125, 135), and in the tropical rain-forests parrakeet flocks are made up of pairs rather than of individuals. With the whistling swan and Canada goose the family groups can supposedly be recognized up until mid-winter.

On the other hand Beebe (15) records the common occurrence of heterotypic flocks in British Guiana, one of which has already been cited. Similarly heterotypic flocks of migrating birds which contain only one representative of a given species are not formed from the junction of family groups. Sherman (186), a careful observer of bird habits, gives much detailed data to show that not all flocking is on the family basis. One who knows the egg-laying habits of cowbirds would expect their flocking to be by individuals. Bobolinks and goldfinches begin the formation of their autumn flocks by the congregating of old males. Chimney swifts, a pre-eminently flocking species, leave their nests by ones and twos to join the immense post-breeding flock.

Here then we have evidence that bird flocks are not always based on the family as a unit. Thus in these more highly organized groups, the individual may be the unit, just as in the aggregations of isopods and brittle starfish. It may be that the highest types of social organization, such as occur in ants and termites, with their development of different types of neuters, come about only through a persistence of family relations, but it is also true that well integrated social groupings arise merely from the aggregation of individuals.

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POLYEMBRYONY IN ANIMALS

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I. INTRODUCTION

THE fact that an egg may, under certain conditions produce two or more embryos is perhaps no more remarkable than that an egg will form a single individual. The developmental factors involved in the production of the individual embryo must be the same in both cases. Nevertheless, the discovery that multiple embryos develop from the egg of a given species has served to arouse the interest of biologists.

In the zoological literature the term polyembryony has been applied to cases in which two or more individuals develop from a single egg during the course of its early development. The term was first used by botanists, and among plant embryologists is applied to all cases in which multiple embryos are formed in the embryo sac, irrespective of the origin of the embryos. Thus in plants multiple embryos (polyembryony) may arise from two eggs, or from the splitting of one egg, or from any one of the following sources: nucellus integument, synergids, antipodal cells, endosperm cells, suspensor. Animal embryologists use the term in the restricted sense only, that is, it is applied by them to cases in which the several embryos develop from one egg.

Some objections have been offered to the term polyembryony, especially in applying it to cases of twinning in animals. But so long as the term is used in a purely descriptive sense, and without implying any particular mode of development, there can be no serious objections to its universal application. Twinning itself must be regarded as the simplest type of polyembryony. That this is true, has been demonstrated in one of the parasitic hymenoptera, to which reference is made below.

Three types of polyembryony may be recognized. These are: (1) Experimental polyembryony, or the production of multiple embryos by artificial means; (2) accidental or sporadic polyembryony, or the occasional production of multiple embryos in a species in which development is typically monembryonic; (3) specific polyembryony, or the habitual production of multiple embryos in a given species.

Among the first to produce experimentally two or more embryos from the egg was Haeckel ('69). He cut into pieces the blastulae of *Crystallodes* and obtained from the larger pieces normal larvae. Since then there have been many successful experiments of a similar nature. Among these may be mentioned the work of Wilson ('93), who isolated the blastomeres of the eggs of *Amphioxus* by shaking, and found that such separated cells were capable of forming complete embryos; the classical experiments of Driesch, and of others, on the eggs of Echinoderms; the studies of Schultze ('95), Herlitzka ('97), and Spemann ('01, '03) on Amphibian eggs; and more recently, the interesting work of Stockard ('21) in producing twins and double monsters in the fish egg by lowering the developmental rate.

The results of these, and many similar

experiments, have brought out some very significant facts with reference to the behavior of isolated blastomeres The behavior of separated blastomeres of the eggs of different species is strikingly different Furthermore, the blastomeres of the same species behave differently at different stages of development Thus, isolated blastomeres of the 2- or 4-celled stage of *Amphioxus* develop into whole embryos, while a blastomere of the 8-celled stage is incapable of forming a complete embryo The same is true of the blastomeres of the Nemertine egg On the other hand, the isolated blastomeres of the Ascidian egg never produce a complete larva, but only partial larvae The blastomeres of such forms are therefore not totipotent

Apparently, these differences are dependent upon the degree of organization of the egg, or of the blastomeres at the time of their separation For example, the undivided Ascidian egg is highly organized, and hence if the blastomeres are isolated, even at a very early stage, they are incapable of producing complete individuals, but only parts of individuals On the other hand, in forms like *Amphioxus* the uncleaved egg is not so highly organized, and consequently the isolated blastomeres of the 2- and 4-celled stages are able to produce whole embryos By the time the 8-celled stage is reached, the organization becomes more or less established, and each of the several blastomeres has attained a definite value as an organ-forming region, and is no longer totipotent The results of such experiments have been used by various writers to explain polyembryony It is probable that certain cases, especially sporadic polyembryony, may arise in nature by the accidental separation of the early cleavage cells, but specific polyembryony can not be explained in such a simple way

Sporadic polyembryony occurs among both the invertebrates and the vertebrates It usually appears in the form of twins, or in the closely related form of double monsters Cases have been reported among cestodes, coelenterates, echinoderms, annelids, and arthropods, but most of the cases cited in the literature are found among the vertebrates Twins or double monsters have been reported in every class of the vertebrates, from the lowest to the highest Even in man it is found in the familiar cases of 'identical twins'

Specific polyembryony also occurs among invertebrates and vertebrates It has arisen independently in several distinct groups of organisms The four outstanding cases are the following (1) Embryonic fission in the Cyclostomatous Bryozoa, (2) Twinning in the Earthworm, (3) Polyembryony in the Parasitic Hymenoptera, (4) Polyembryony in the Armadillos

1 EMBRYONIC FISSION IN CYCLOSTOMATOUS BRYOZOA

Among the Cyclostomatous Bryozoa there has been described a process termed "embryonic fission" which clearly belongs to the category of polyembryonic development This process was discovered by Harmer, who first announced his discovery in 1890 in a preliminary communication to the Cambridge Philosophical Society In 1893, after having studied the development of several species belonging to the genus *Crisia*, he published his final results A few years later ('96, '99), Harmer extended his studies to two other genera, *Lichenopora* and *Tubulipora* In 1903 Dr. Alice Robertson published an interesting paper entitled "Embryology and Embryonic Fission in the Genus *Crisia*" She confirmed the chief results of Harmer concerning the budding of the embryo, the separation of these buds

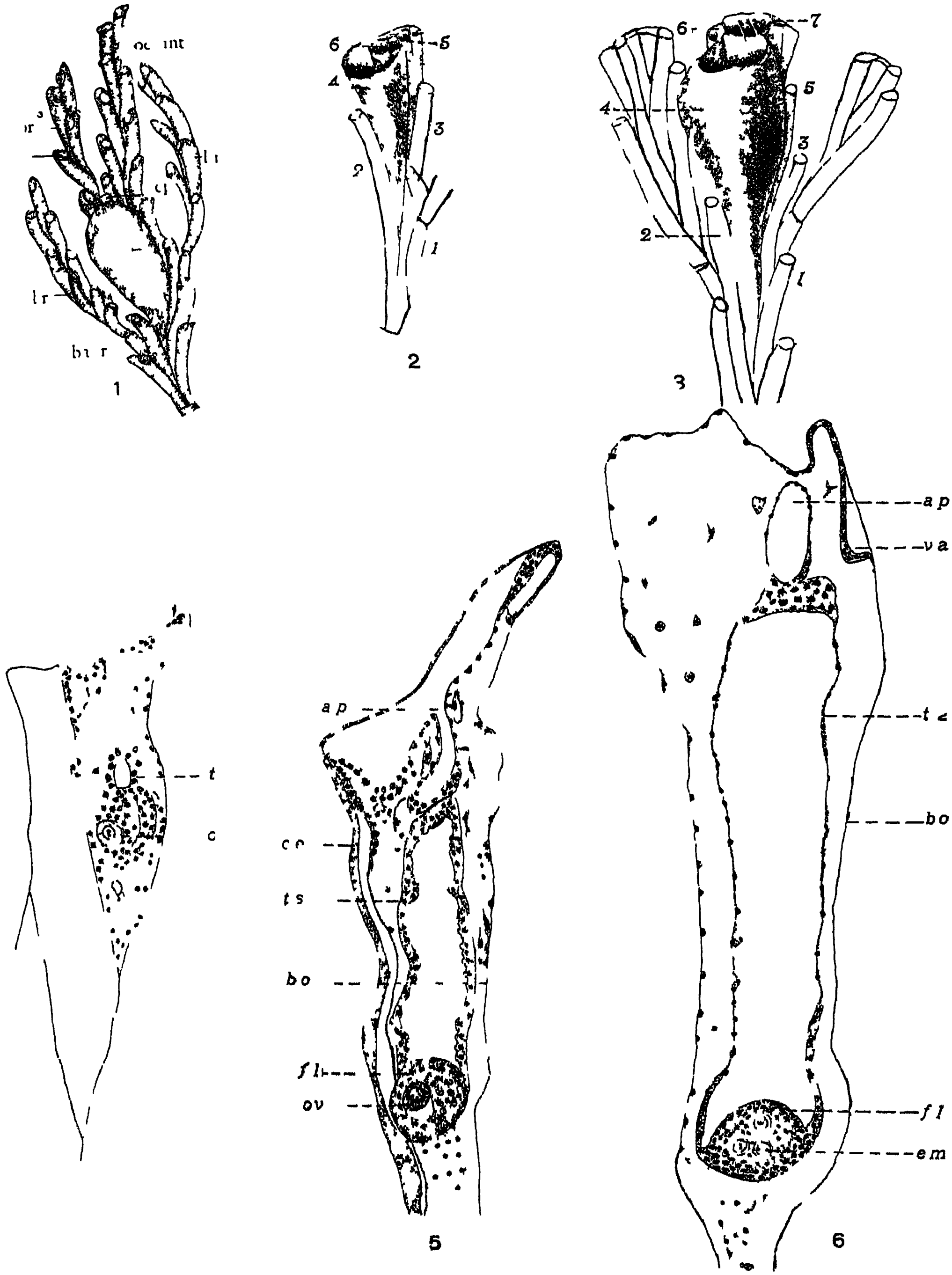


FIG 1 A portion of a colony of *Crisia occidentalis*, showing the branching of the ooecial internode The ooecium is the fifth member of the internode (Robertson)

FIGS 2 AND 3 Two stages showing the development of the ovicell in *C remota* The ovicell is numbered 4 in each figure (Harmer)

FIG 4 A median longitudinal section of a young ovicell of *C eburnea* The ovum is partially surrounded by a polypide bud (Harmer)

FIG 5 A similar section of *C remota*, showing the ovum surrounded by the follicle formed from the polypide bud *ap*, aperture, *c e*, calcified ectocyst, *b o*, back of ovicell, *t s*, tentacle sheath, *fl*, follicle, *ov*, ovum (Harmer)

from the mother embryo, and their ultimate transformation into free swimming larvae. She also added several new points of interest, such as the origin of germ cells, and the establishment of the fact that certain species are dioecious. Robertson worked on four species of the genus *Crisia: C. geniculata, C. occidentalis, C. edwardsiana, and C. franciscana.* Unfortunately, in her paper on the embryology of *Crisia*, Robertson incorrectly identifies the last three species. This error was corrected several years later in her systematic paper (1910). In the embryology paper the three species in question were identified as *C. eburnea, C. cornuta, and C. occidentalis*, respectively.

The Bryozoa, which are sometimes called moss-animals, are mostly marine, and are usually colonial. Superficially, they resemble hydroids, but in structure are strikingly different from hydroids. The phenomenon of polyembryony occurs quite generally throughout the sub-order of Cyclostomata. The colonies of this sub-order are characterized by great simplicity of structure. In the genus *Crisia* each colony is composed of many branches. A branch is made up of a series of internodes, each of which possesses several calcareous tubes, called zooecia (fig. 1). Within each zooecium is found the polypide, or soft parts of the individual. The polypide consists of a mouth, surrounded by a circle of ciliated tentacles, and an alimentary canal, composed of the oesophagus, stomach, and intestine.

The egg develops in a specialized zooecium, called an ooecium or ovicell (fig. 1, *oe*). The ovicell begins its formation at a very early stage of the zooecium. It is the result of a successful union between an ovum and the young polypide-bud. The ovum becomes united to the base of the stomach of the polypide-bud by the means of a strand of mesoderm called the funiculus. If the union is successful, the polypide, as such, becomes aborted, later forming a "follicle" about the developing embryo. The fertile zooecium then develops into an ovicell, which serves as a brood chamber for the developing embryos and larvae. Under these conditions the egg, instead of producing a single larva, proceeds to fragment or bud; each bud, either secondary or tertiary, or embryo develops into a larva. In this manner a single egg may produce more than 150 larvae. The secondary embryos remain within the ovicell until they have become ciliated larvae, and upon being set free each is capable of forming a new colony.

The following account of polyembryony in Bryozoa is based chiefly on *Crisia remosa*, as described by Harmer. It is probably true, as Robertson suggests, that some of his earliest stages do not necessarily represent eggs which would have produced embryos (*e.g.*, figs. 4, 5).

The germ cells. According to Robertson ('03), the germ cells in *Crisia* arise in the mesodermal layer and are produced at the edge of the growing tip of the terminal internode of the colony. They are differentiated at a point lying anterior to the budding zone. This occurs earlier than the origin of the polypide-buds. In the male colonies of a dioecious species, such as *C. occidentalis*, a few germ cells become attached to each developing bud, and thus give rise to the testis. In most cases the testis probably degenerates before forming mature spermatozoa.

In the female colonies the ovaries likewise develop at the anterior edge of the young tips, and, as in the male colonies, the germ cells must unite with a polypide-bud in order to mature. Many ova never form this union, and consequently soon degenerate. In some cases the polypide-

bud develops, while the attached ovum degenerates, either before or after having passed through the first cleavage stages. In other cases the attached ovum gains the ascendency, while the polypide-bud becomes aborted, and forms a follicle about the growing embryo.

The ovicell. As already stated, the ovicell is a specialized zooecium in which the development of the embryo takes place. Smitt ('65) was the first to show that the ovicell forms in a manner similar to that of the zooecia, but to Harmer ('93) belongs the credit of having pointed out that it is the morphological equivalent of a zooecium. In *C. remosa* the growing ovicell occupies the fourth unit of the young internode, the rest of the units being ordinary zooecia. In *C. eburnea* ovicell-bearing internodes have six zooecia and the ovicell. The latter takes the place of the second or third zooecium in an internode having no ovicell. Figures 2 and 3 show two stages in the development of the ovicell in *C. remosa*. The positions of the ovicell and the ordinary zooecia are indicated by the numbers. The ovicell is number 4 in each figure.

Fertilization and cleavage. The processes of maturation and fertilization have never been observed, but it is assumed by Harmer that inasmuch as mature spermatozoa are formed, fertilization must occur normally. Robertson believes that if fertilization does occur, it must take place near the time at which the ovum and the polypide-bud unite. In view of the probable degeneration of the testis, she suggests the possibility of parthenogenetic development.

The cleavage divisions occur while the ovicell is still undergoing development. At the time the ovum becomes surrounded by the polypide-bud the tentacle-sheath is scarcely developed (fig. 4, *ts*). In figure 5 is shown a stage in which this sheath has increased considerably in size, while the ovum is still undivided. The polypide-bud has been transformed into a "follicle," in which the cells are arranged about the ovum in concentric layers. Soon after this stage the ovum begins to divide, apparently irregularly, to form blastomeres. A three-celled stage is shown in figure 6. The three blastomeres are separated from one another and an ingrowth of follicular cells has migrated in between them. It is characteristic of all of the early cleavage stages of *Crisia* for the blastomeres to become completely separated.

The interpolation of follicular elements between the cleavage cells is a characteristic feature of the early development of *Crisia*, and as a result, the blastomeres undergo division independently of one another, that is, there is no regularity in the succession of cleavage cells. The process of segmentation continues in this manner until about twenty to twenty-four cells are formed, after which the blastomeres become collected into a compact mass. In the meantime, important changes have taken place in the growth of the ovicell. The tentacle-sheath has grown to such a size that it now practically fills up the entire cavity of the ovicell, and the follicle likewise has greatly increased, producing knob-like projections that extend into the cavity of the tentacle-sheath.

The nutriment for the rapid growth of these parts is obtained very largely at the expense of the neighboring zooecia. These have a series of intercommunicating channels which are formed by means of strands of funicular tissue that pass through pores perforating the calcareous ectocyst. The ovicell and its contiguous zooecia likewise communicate by the organic connections and through these channels the nutriment for the rapidly

growing embryo and follicle is drawn from the zooecia, which sometimes atrophy as a result It is only in this manner that one can give a rational account of the rate of development of the ovicell, and can further explain the formation of a massive primary embryo from the minute egg of *Crisia*

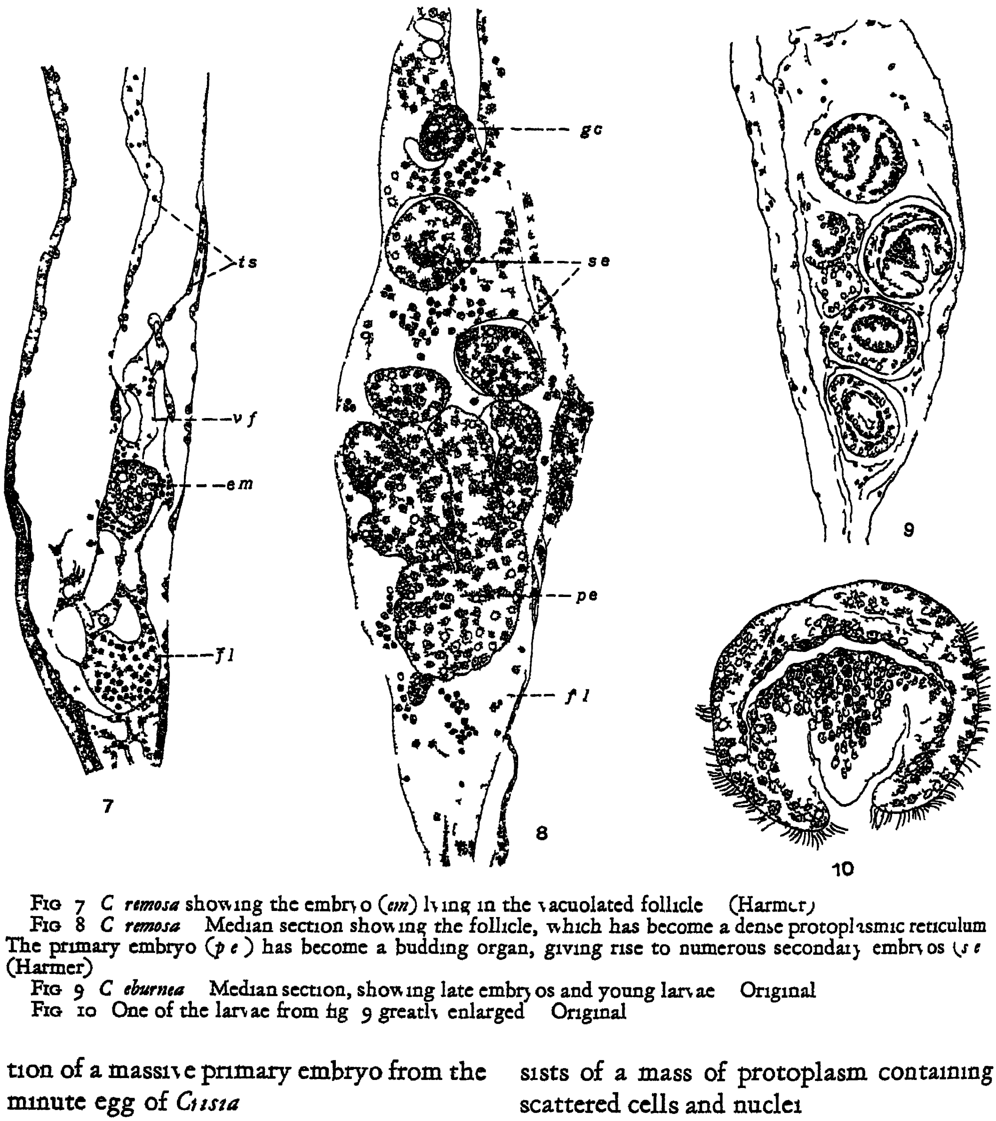


FIG 7 *C remosa* showing the embryo (*em*) lying in the vacuolated follicle (Harmer)
FIG 8 *C remosa* Median section showing the follicle, which has become a dense protoplasmic reticulum The primary embryo (*p e*) has become a budding organ, giving rise to numerous secondary embryos (*s e*) (Harmer)
FIG 9 *C eburnea* Median section, showing late embryos and young larvae Original
FIG 10 One of the larvae from fig 9 greatly enlarged Original

The primary embryo The separation of the blastomeres during the earliest stages of development is undoubtedly associated with the nutrition of the embryo, and the collecting together of the cells at a later period to form the ball-stage is due to the dissociation of the interpolated follicular elements to form nutritive material which is consumed by the embryo During this period, the embryo gives no evidence of differentiating into germ layers, but consists of a mass of protoplasm containing scattered cells and nuclei

The ball-stage is constant for all Cyclostomata For some time the embryo remains practically unaltered, but the surrounding follicle is transformed from a solid structure to a protoplasmic retic-

ulum (fig 7, *fl*), which eventually fills up a large part of the cavity of the ovicell The formation of the reticulum is first seen in the development of vacuoles in the solid follicle In the organization of the protoplasmic reticulum from the follicle is to be seen the formation of a nutritive mechanism for the numerous larvae which will later arise from the primary embryo The primary embryo itself is formed from the ball-stage by an increase in size of the latter In some species this increase in size may enlarge the ball from 40 to as much as 200 microns

The secondary embryos The secondary embryos arise by a process of budding from the primary embryo, which becomes a distinctly budding organ The simplest type of budding occurs in *C remosa* and in *C denticulata* In *C remosa* the distal end of the primary embryo sends upward several finger-like processes, which by a series of constrictions bud off secondary embryos into the reticulum (fig 8, *s e*)

A variation of this simple method of budding is found in *C occidentalis* In this species buds may arise at any point on the surface of the primary embryo In *C franciscana* still another method of budding is found The primary embryo first breaks up into relatively large masses of cells, or secondary embryos, and these in turn give rise to budding centers from which tertiary embryos are formed

In all of these species the budding organ continues active during the entire functional period of the ovicell, even until some of the older secondary embryos have matured into free-swimming, ciliated larvae Ultimately, the primary embryo itself forms a larva

The larvae Soon after the secondary (or tertiary) embryos are cut off from the primary embryo or budding organ, they differentiate into a two-layered condition, and undergo further development within vacuoles of the protoplasmic reticulum There are also found in some of the vacuoles the giant-cells, which are multinucleated elements formed from the thickened distal end of the tentacle sheath Apparently, they perform the function of excavating spaces in the follicular tissue in which the larvae can undergo development

Of the two layers of which the young larva is composed, the inner one, according to Harmer, is probably mesoderm The free-swimming larva is completely developed within the ovicell, and at maturity has a cylindrical-shaped body with an aperture on one side that leads to the sucker (figs 9, 10) It is composed of the two layers, and has the greater portion of the outer surface covered with long cilia Upon reaching maturity, the larvae puncture the membrane covering the tubular aperture of the ovicell and thus escape into the surrounding medium Here each larva is capable of attaching itself to some object by means of the sucker, and of producing a colony characteristic of the species to which it belongs

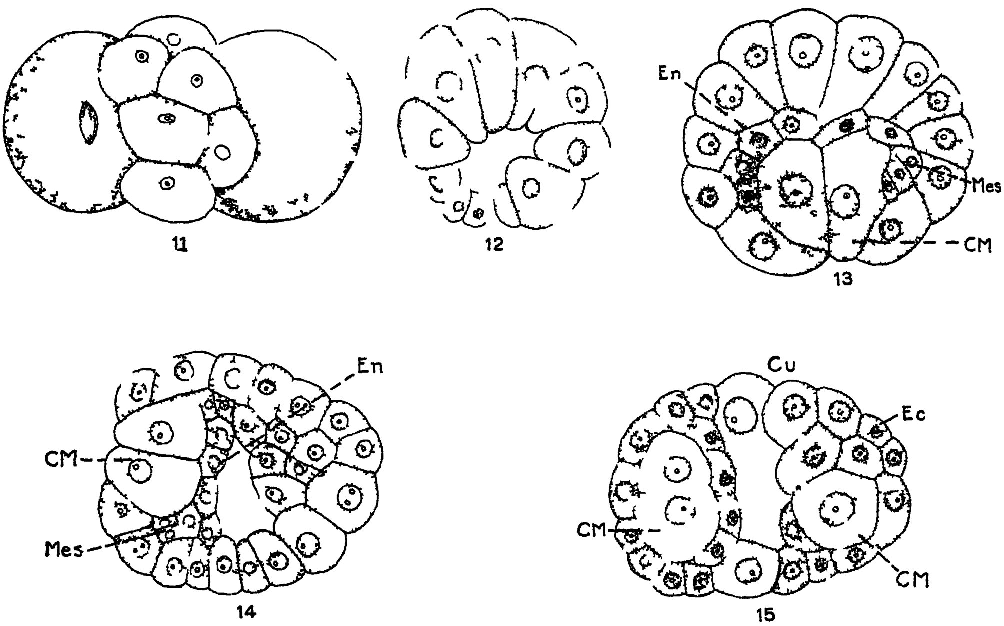
3 TWINNING IN THE EARTHWORM

The formation of twins in the earthworm deserves consideration in any general review of polyembryonic development, even though it has not been demonstrated that all of the eggs of the species concerned show this method of development Several different investigators have reported the discovery of embryonic bifurcation in the Oligochaeta, since Dugès first observed and described a double monster of *Lumbricus trapezoides* in 1828 All of the cases so far reported, with the exception of two, fall within the highest family of the Oligochaeta, namely, the Lumbricidae. In 1921 Welch reported the occurrence of bifurcation in the embryos of one of the common tubi-

ficids, *Tubifex tubifex*, belonging to the family Tubificidae Penners (24) has recently described the development of double embryos in *Tubifex rivulorum* Hague (23) reports the discovery of bifid embryos in *Sparganophilus eiseni* thus adding a third family (Glossocolecidae) in which this type of development is found

first changing into flattened plates and finally disintegrating completely

The cleavage of this egg, like that of many other earthworm eggs, is variable, and consequently it was not possible for Kleinenberg to follow accurately the early history of development The first division produces two large blastomeres and while there sometimes follows a three-



FIGS 11–15 EARLY STAGES OF *Lumbricus trapezoides* (AFTER KLEINENBERG)

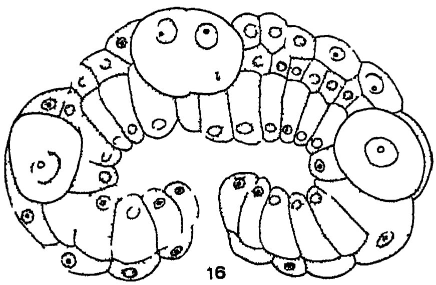
FIG 11 Early cleavage stage seen from above, showing two large and six smaller cells FIG 12 Section of the blastula stage, or germinal bladder FIG 13 Section of solid germinal sphere, showing the rudiments of the layers of the first embryo FIG 14 Late stage in which the formation of the second embryo has begun FIG 15 Section of young twin embryos The one on the right is farther developed than its co twin on the left

For our knowledge of the early development of twins in earthworms we are dependent almost wholly upon the account of Kleinenberg ('78, 79) on the embryology of *Lumbricus trapezoides* (*Helodrilus caliginosus trapezoides*) He found that while the number of eggs deposited in the cocoon, or egg capsule of this species varies from three to eight, yet a single egg usually developed The rest of the eggs apparently are not fertilized, and soon undergo degeneration,

celled stage, the general rule is for each of the two blastomeres to give off in succession three small cells The six small cells thus formed come to lie above and between the two larger blastomeres (fig 11) By a series of somewhat irregular divisions, affecting the large as well as the smaller blastomeres, the egg develops into a blastula, or "germinal bladder" This blastula is remarkable for having its cavity, the blastocoel, frequently open to the outside by a cleavage-pore, situated

at the lower pole (fig 12) The blastula is soon transformed into a solid sphere (fig 13) This is brought about through the differentiation of two large cells (primary mesoblasts) which push into the cavity and become covered over by small blastomeres From these cells the first rudiments of the entoderm and mesoderm are derived The cell mass then elongates in the direction of the two poles While mesoblasts (fig 14, *c m*) develops somewhat in advance of the opposite end, but eventually both ends become equally well differentiated (fig 15)

Gastrulation takes place by an invagination of the entoderm This process begins at the lateral margins of the furrow or groove in both hemispheres, and results in producing two gastrulae, which are held together by the median cord of large



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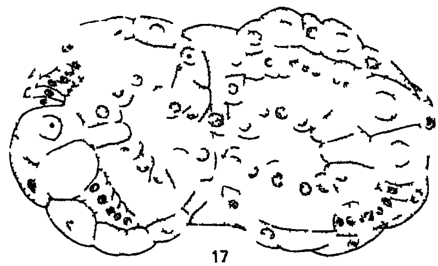

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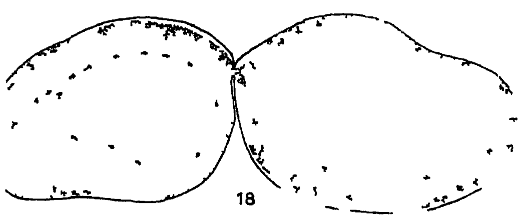

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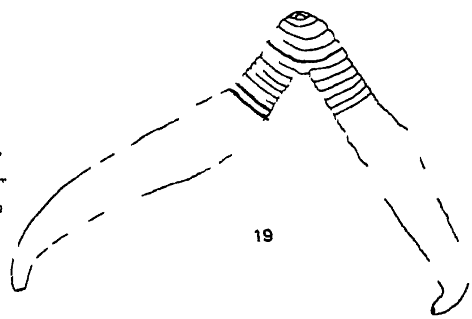

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FIG 16 Longitudinal section of a double embryo, in profile (After Kleinenberg)
FIG 17 Longitudinal horizontal section of a double embryo (After Kleinenberg)
FIG 18 Two embryos about to break apart Original
FIG 19 Double monster, produced as a result of the failure of the embryos to separate from each other Original

the elongation of the egg is in progress, a transverse furrow appears, mid-way between the two poles This furrow does not extend around the entire circumference, but cuts in from one side only The furrow continues to deepen until finally the two hemispheres of the egg are held together only by a few enlarged ectodermal cells (fig 15, *cu*) In the meantime, the cell mass undergoes further differentiation The end containing the large primary ectodermal cells (fig 16, 17) While thus connected, the two embryos complete their internal organization and development They usually succeed in freeing themselves from each other by a series of rotations (fig 18), which result in breaking the attenuated, connecting cord If for any reason the cord should fail to break, double monsters, showing various degrees of union, are produced (fig 19)

A second type of abnormality is some-

times found during the gastrula stage. It consists in the formation of a small bud on the margin of the mouth of the gastrula. It is probably the result of a very unequal development of the two halves of such stages as that shown in figure 14.

A survey of the literature on the occurrence of twinned embryos in earthworms indicates clearly that in most of the species studied twinning is rather rare. The species in which it has become a common phenomenon is *Lumbricus trapezoides*, now known as *Helodrilus caliginosus trapezoides*. Indeed, Kleinenberg regarded the gemelliparous development in this species as universal. On the other hand, Vejdovsky ('88–'92) maintained that the development of two embryos from one egg is abnormal; he therefore suggested the possibility that the abnormal development may be due to changes in temperature and moisture. In this connection, the observations of Weber ('17) on this species are of interest. Out of 184 cocoons examined, 1 contained four embryos, 101 two individuals each, 57 only one each, and 25 had eggs in various cleavage stages. Thirty-five of the 101 cases had various types of monsters.

Any future work on twinning in earthworms should involve a study of a much more complete series of early stages than any previous worker has been able to obtain, chiefly with the view of finding a possible relationship between the cleavage phenomenon and the twinned embryos. Furthermore, in the light of Vejdovsky's suggestion, such studies should include experiments carefully planned to determine what influence, if any, changes in temperature, moisture, and air may have on the production of double embryos.

4. POLYEMBRYONY IN THE PARASITIC HYMENOPTERA

Since the discovery of polyembryony in insects by Marchal in 1898, there have appeared a number of papers dealing with this type of development in the parasitic Hymenoptera. Marchal's main paper ('04) gave the first clear description of polyembryony. It presents an account of the development of *Encyrtus fuscicollis* and *Polygnotus minutus*, together with the suggestion that *Ageniaspis testecipes* must also develop by polyembryony.

In 1906 Silvestri published a very important paper on the development of *Litomastix truncatellus*. He demonstrated that the egg of this parasite produces on the average about 1500 sexual individuals, in addition to a number of the so-called asexual larvae which are non-viable. Following this, Silvestri issued a series of papers dealing with the embryology of various species of parasitic Hymenoptera, both monembryonic and polyembryonic.

In 1914, Martin published a paper on *Ageniaspis fuscicollis*. This paper deals with the very early stages of the egg.

In 1915 the writer published an account of the late stages of development of *Copidosoma gelechiae*, and since then a series of papers covering the development of *Paracopidosomopsis floridanus*. The latter, a common parasite of the cabbage looper *Autographa brassicae*, was described by Ashmead as a distinct species, but according to Leiby ('22, p. 198), Dr. L. O. Howard, Mr. A. B. Gahan, and others regard this species as identical with *Litomastix* or *Copidosoma truncatellum*. A short paper dealing with the biology and sex ratios of *Platygaster felti*, a species which also develops by polyembryony, was published in 1921.

In 1922 Leiby published a very complete account of the polyembryonic development of *Copidosoma gelechiae*. Leiby and Hill ('23, '24) have described the development of two species belonging to the family Platygastridae, namely, *P. hiemalis* and *P. vernalis*, both of which are parasites of the Hessian fly.

In addition to the above publications, there are many references in the literature to species some of which undoubtedly develop by the process of polyembryony. In the following table (table I) an attempt is made to include all of the undoubted polyembryonic species. The first column gives the name of the polyembryonic species, the second the name of the host insect, the third the average number of individuals in a brood, and the fourth the observer.

several species so far investigated, but there are also striking differences. Many of the accounts so far given for the development of polyembryonic insects are incomplete, and for this reason it is difficult to prepare a review covering such important questions as the origin and evolution of this type of development in the Hymenoptera. However, the recent observations of Leiby and Hill ('23) indicate that polyembryony in insects begins as a twinning process, in which the egg, at an early stage, divides into two parts, each of which ultimately forms a complete individual. As the number of individuals arising from the egg (of different species) increases, the process becomes more and more complicated, finally culminating in a highly specialized mode of development. It will be necessary, perhaps, to study in detail the development of several more species before a correct view of the evolution of polyembryony in insects can be reached. In

TABLE I

PARASITE	HOST	BROOD	OBSERVER
Platygaster hiemalis	*Phytophaga destructor*	2	Leiby and Hill, '23
Platygaster vernalis	*Phytophaga destructor*	8	Leiby and Hill, '24
Platygaster felti	*Walshomyia texana*	11	Patterson, '21
Platygaster felti	*Rhopalomyia sabinae*	18	Patterson, '21
Polygnotus minutus	*Phytophaga destructor* *Phytophaga avenae*	11	Marchal, '04
Ageniaspis fusciollis subspecies *praysincola*	*Prays oleelus*	14	Silvestri, '08
Ageniaspis testaceipes	*Lithocolletis cramerella*	13	Marchal, '04
Ageniaspis fuscicollis	*Hyponomentus malinellus*	100	Marchal, '04
Encyrtus variicornis	*Anarsia lineatella*	28	Sarra, '15
Copidosoma buyssoni	*Coleophora steffani*	58	Silvestri, '14
Copidosoma sp.	*Olethreutes variegana*	148	Sarra, '18
Copidosoma gelechiae	*Gnorimoschema gallaesolidaginis*	163	Leiby, '22
Copidosoma gelechiae	*Gnorimoschema salinaris*	191	Patterson, '15
Paracopidosomopsis floridanus	*Autographa brassicae*	1161	Patterson, '17
Litomastix truncatellus	*Plusia gamma*	1481	Silvestri, '06
Copidosoma tortricis	*Tortrix comariana*	?	Waterson, '22
Berecyntus bakeri	*Euxoa auxiliaris*	1289	Snow, '25
Aphelopus theliae	*Thelia bimaculata*	50	Kornhauser, '19

The species listed in the table belong to three families of the parasitic Hymenoptera, namely Encyrtidae, Platygastridae, and Dryinidae. Further investigations will undoubtedly bring to light many additional polyembryonic species. The reviewer has observed four or five unidentified species in which certain phases of development strongly suggest that they are polyembryonic.

There are many points of similarity in the method of development as found in the

the meantime, it is possible to indicate in outline the general trend of the process in this group. This can be done best by considering first twinning in the egg of *Platygaster hiemalis*.

Twinning in Platygaster hiemalis

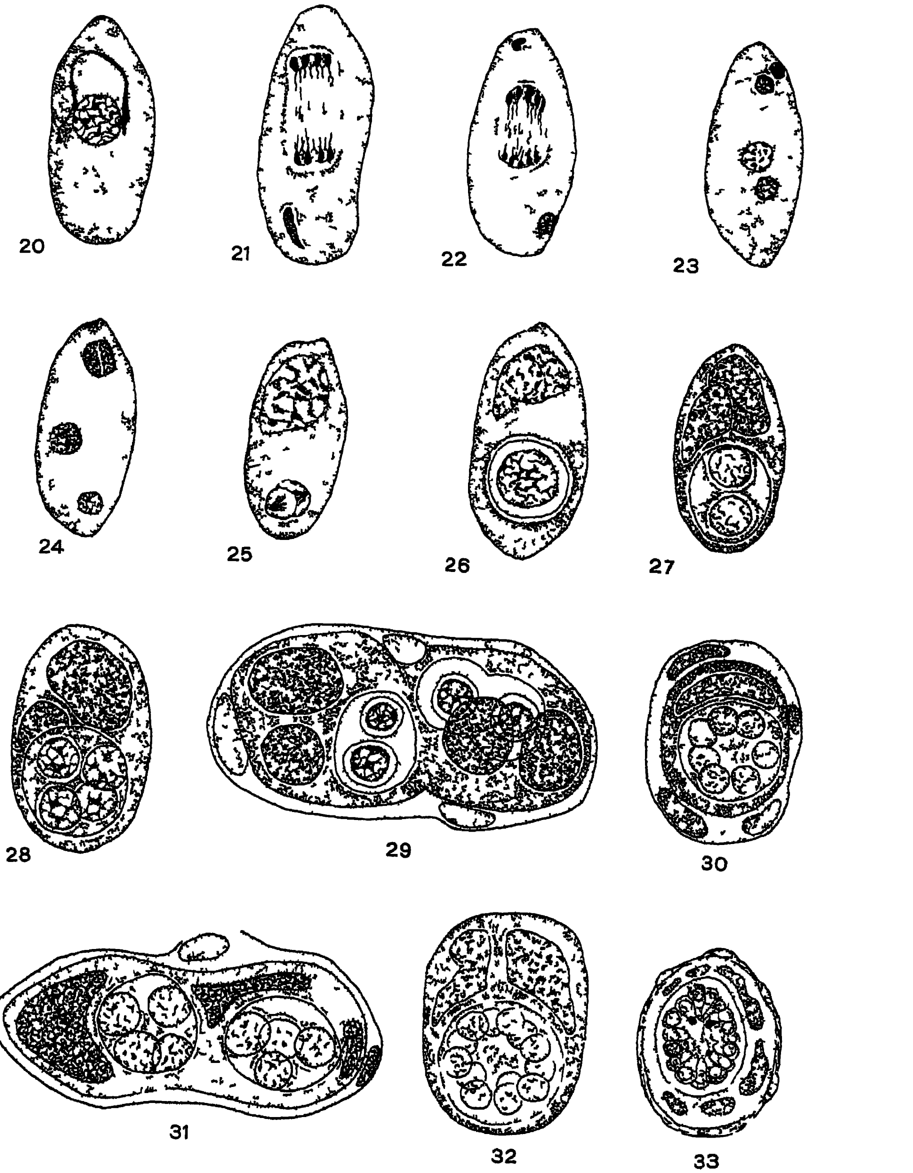
Platygaster hiemalis is a parasite of the Hessian fly, the well-known pest of wheat. Leiby and Hill ('23) have shown that its egg develops either monembryonically or polyembryonically. The parasite lays from four to eight eggs in the egg or young larva of the host. Some of these eggs give rise to single embryos, others develop into twins, while still others degenerate. Some eggs of the group of four to eight are inseminated, while others are unfertilized.

The freshly deposited egg is ovoid in shape, with a rounded posterior end and a somewhat pointed anterior end. The spherical nucleus is situated near the center of the egg. If the egg is fertilized, a single elongated sperm is present in the cytoplasm (fig. 20). But whether fertilized or not, the egg undergoes two typical maturation divisions, during which reduction in the number of chromosomes occurs (figs. 21, 22). The two polar body nuclei are not eliminated from the egg, but remain for a while as condensed masses at its anterior end (fig. 23). They soon unite to form a very large, single polar nucleus, or the paranucleus of Marchal (figs. 24, 25).

After maturation is completed, the female pronucleus moves toward the posterior end of the egg, where it unites with the sperm nucleus to form the cleavage nucleus, or in case the egg is unfertilized, the female pronucleus becomes directly the cleavage nucleus. Apparently, the presence of the sperm in the cytoplasm does not modify either maturation or the type of development which follows. Fertilization does, however, determine the sex of the resulting individuals, for in common with many other hymenoptera, the unfertilized eggs of polyembryonic species give rise to haploid males, developing by what has been called facultative parthenogenesis. The fertilized egg presumably gives rise to females. This point, however, has not been fully established.

About twenty-four hours after the beginning of development, the egg becomes differentiated into two distinct regions, the polar region and the embryonic region. The embryonic region, which eventually gives rise to the embryos, is situated in the center of the posterior half of the egg. It stains lighter than the rest of the egg and contains the cleavage nucleus (fig. 26). All of the rest of the egg comprises the polar region, in the anterior portion of which is found the large paranucleus. The polar region has been termed the trophamnion, chiefly because of its function of absorbing and elaborating the host tissues for the purpose of nourishing the parasitic embryos until they are able to feed for themselves. The absorption of food from the host tissue is facilitated by the change which takes place in the distribution of the several parasitic eggs. Sometime during the early part of the second day the group of from 4 to 8 eggs deposited in the host by the parasite becomes dispersed throughout the body cavity of the host embryo or larva, and during the process of scattering each egg comes in contact with certain host tissues which partially or wholly surround it. The eggs are now called parasitic bodies. About one-third of the eggs deposited do not develop, apparently because they fail to become surrounded by the tissues of the host.

Just prior to the division of the embryonic or cleavage nucleus the polar



FIGS 20–33 SHOW VARIOUS STAGES OF THE DEVELOPMENT OF THE EGG OF *Platygaster hiemalis* (AFTER LEIBY AND HILL)

Fig 20 Egg showing nucleus and sperm Fig 21 Egg four hours old showing sperm and first maturation spindle Fig 22 Egg seven hours old, showing second maturation spindle, first polar body (above), and sperm nucleus Fig 23 Egg shows the two polar bodies, and the male and female pronuclei Fig 24 Same as above except that polar-body nuclei are fusing Fig 25 Egg with pronuclei fusing and large polar nucleus Fig 26 Egg showing the embryonic region differentiated from rest of cytoplasm Fig 27 Parasitic body three days old, with two nuclei in embryonic area, and two paranuclear masses Fig 28 A parasitic body with four embryonic nuclei Fig 29 A longitudinal section through the twinning stage The embryonic region has divided and each half has received two nuclei Fig 30 Embryo in early blastula stage Seven of the sixteen nuclei are seen in the section Fig 31 A twin germ, which is surrounded by the cyst of host tissue The trophamnion has not yet divided Fig 32 A 32-celled blastula of an egg developing monembryonically Fig 33 Late blastula stage of embryo

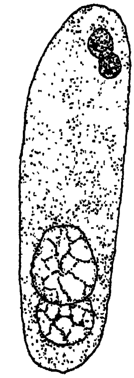
nucleus divides amitotically to form two paranuclear masses. The first division of the embryonic nucleus occurs on the second day (fig. 27), and the second divisions take place between the fourth and fifth days of development (fig. 28). At this point one of the paranuclear masses migrates to the posterior end of the parasitic body and divides, while the one remaining at the anterior end also divides. There are now four of these masses, two at each end of the trophamnion. These divisions result in changing the shape of the parasitic body from oval to elongate. Evidently, this change in shape is one of the developmental steps leading to the production of twins, for the parasitic bodies in which it occurs proceed immediately to divide into two parts, each of which forms an embryo. The embryonic region is the first to be affected by the division. It divides into two equal parts, each part receiving two of the four embryonic nuclei (fig. 29). Each half of the divided embryonic region constitutes a true germ, which will eventually develop into a parasite.

The division of the embryonic region to form two germs is followed by the appearance of a constriction about the middle of the trophamnion (fig. 29). This constriction finally completely divides the trophamnion, and although the two halves thus formed are held together for some time by the cyst of host tissue, yet the two germs develop independently of each other. The nuclei of each germ divide to produce four (fig. 31), then eight and finally sixteen nuclei. The sixteen nuclei arrange themselves in the form of a hollow sphere, thus forming a typical early blastula stage (fig. 30). In the course of further development, the embryonic nuclei continue to divide, and cell walls come in to change the early blastula into a cellular blastula (fig. 33).

Not all eggs deposited by the female parasite produce twin embryos, but as Leiby and Hill have shown, some develop monembryonically. Apparently, all of the eggs develop in a similar manner up to the point at which four embryonic nuclei are present. If the egg is to form but one embryo, a division of the embryonic region at the four-celled stage does not take place, but instead the cleavage nuclei continue to multiply (fig. 32) until a single blastula is developed.

It will not be necessary to follow in detail the development from the blastula to the adult stage. The embryos reach an advanced stage of development during the fall months, and pass the winter in the body of the host. Their development is continued again in the early spring, and during the latter part of the spring, each embryo, upon attaining the larval stage, ruptures the trophamniotic membrane. The free larvae feed upon the host tissues, finally consuming the entire contents of the host. The fully formed larvae remain within the body wall of the host during the early summer, and each embryo forms a pupal cell in which it transforms into a pupa. The adult parasites emerge from the host carcass and puparium in the early fall, at a time when they are able to find and parasitize freshly deposited eggs of the second generation of the Hessian fly.

The type of development exhibited in *Platygaster hiemalis* is of very great importance to the subject of polyembryony in insects. Interest in the case does not rest alone on the fact that it shows the simplest possible type of polyembryony, but also on the fact that some of the eggs develop monembryonically. The monembryonic development in this species is similar to that described for certain monembryonic platygastrids, and represents a very highly specialized type of development. It is probable that without the development



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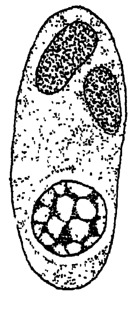

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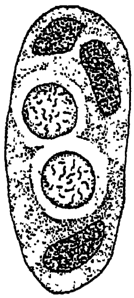

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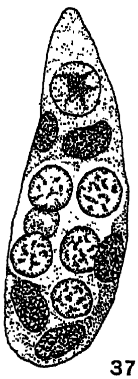

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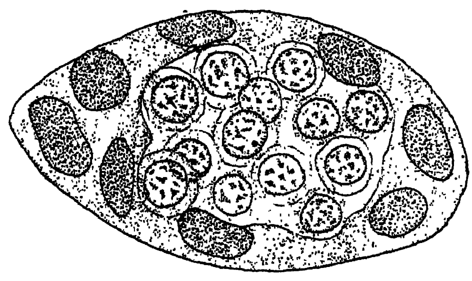

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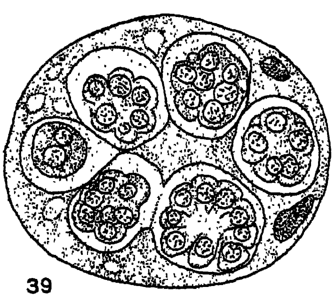

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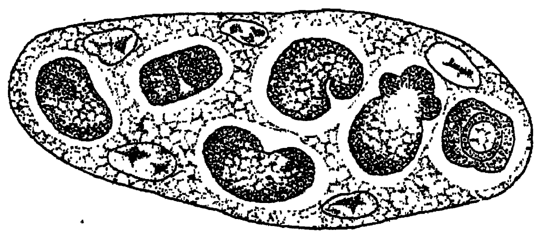

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Figs. 34–40. Show Seven Stages in the Development of *Platygaster vernalis* (after Leiby and Hill)

Fig. 34. A stage showing the fusion of the pronuclei. The two polar bodies are at the upper end. Fig. 35. The embryonic region is differentiated about the cleavage nuclei. The polar body nuclei have become paranuclear masses. Fig. 36. A parasitic body with three paranuclear masses, and the cleavage nucleus ha divided. Fig. 37. A parasitic body five days old, showing five of the eight embryonic nuclei. Fig. 38. A section of a parasitic body, showing thirteen of the sixteen germs. Fig. 39. A section of a thirteen day old polygerm, showing portions of six embryos. Fig. 40. Longitudinal section of a polyembryonal mass about 26 days old.

of this specialized type of monembryony, the parasitic egg would not be able to proceed to the production of polyembryony.

Polyembryony in Platygaster vernalis

A knowledge of the simplest type of polyembryony in *Platygaster hiemalis* is essential to an understanding of that process as it is found in the more highly specialized forms. All investigators familiar with insect polyembryony have recognized the desirability of working out the development in a species in which but a few individuals arise from one egg, say four or eight. No one has described a species with four embryos, but recently one in which about eight embryos develop has been reported on by Leiby and Hill ('24).

The species in question is *Platygaster vernalis*, and like *P. hiemalis* is also a platygastrid infesting the egg of the Hessian fly. While there are many points of similarity in the development of these two parasites, yet there are certain significant differences. The chief differences are as follows: (1) The female of *P. vernalis* deposits but a single egg at each oviposition instead of from four to eight; (2) the parasite egg is placed in the egg of the host in a manner such that it becomes lodged in the mid-intestine of the host larva; (3) the parasitic body of *P. vernalis* never becomes surrounded by a cyst of host tissue; (4) finally, the egg of *P. vernalis* produces on the average about eight embryos, and does not develop monembryonically or produce twins.

The early stages of *P. vernalis* are very similar to those of the preceeding species. The egg is cylindrical in shape and contains the oocyte nucleus and if it has been fertilized, there is present in the cytoplasm a single spermatozoon. The two typical maturation divisions occur, giving rise to two polar-body nuclei (fig. 34). These nuclei do not fuse to form a single polar nucleus, but instead each becomes directly transformed into a paranuclear mass (fig. 35).

The egg is transformed into a parasitic body shortly after the cleavage nucleus is fully organized (fig. 35). A clear area of cytoplasm develops about the cleavage nucleus, and this with the nucleus constitutes the embryonic region from which the embryos arise. The rest of the cytoplasm with the two paranuclear masses is the trophamnion.

Beginning on the second day and extending to the seventh day after oviposition, the cleavage nucleus undergoes four divisions, producing a series of stages characterized by two (fig. 36), four, eight (fig. 37) and sixteen (fig. 38) embryonic nuclei respectively. It sometimes happens that the embryonic nuclei do not divide synchronously at a given division, and consequently there may be less than sixteen nuclei. During this time the trophamnion increases in size and the paranuclear masses also multiply and become evenly distributed throughout the trophamnion (fig. 38). At the end of the fourth division of the embryonic nuclei the parasitic body develops into a typical polygerm. Each embryonic nucleus, after separating from the other, becomes surrounded by a small amount of cytoplasm, about which a cell membrane is formed. A cell thus organized is a germ that will eventually give rise to one or two embryos.

The nucleus of the single-cell germ multiplies by division until eight nuclei are formed when a division of the germ to produce two daughter germs may occur. Not all germs, however, divide. If a daughter germ divides the result is the

formation of a pseudogerm, or small germ which is not capable of further development.

During an early stage of the polygerm strands from the peripheral trophamnion pass toward the center of the polygerm and surround the developing germs or early blastulas (fig. 39). The subsequent stages of development are similar to those of *P. hiemalis*. However, not all of the embryos reach full development, so that the polyembryonic brood averages only about eight individuals. After the primary larval stage is reached, the trophamniotic membrane ruptures, and the free larvae feed upon the chyle or contents of the mid-intestine of the host. The mid-intestine finally ruptures and the so-called secondary or mature larvae feed upon the tissues of the host.

Polyembryony in other species

A knowledge of the primitive types of polyembryony as just outlined for *P. hiemalis* and *P. vernalis* is necessary for an understanding of the more complex types of polyembryony as found in other Hymenoptera, in which from 150 to more than 2000 individuals arise from one egg. The development of three of these complex forms has been worked out in more or less detail. These are *Copidosoma gelechiae* (Patterson, '15; Leiby, '22), *Litomastix truncatellus* (Silvestri, '06), and *Paracopidosomopsis floridanus* (Patterson, '21b). The average numbers of embryos produced per egg in the three forms are 163, 1481, and 1161, respectively (see table I).

The detailed accounts of the development of the complex forms antedate those given for the simpler species. It is now evident that it will be necessary to reinvestigate or reinterpret some of the late stages of development of such forms as *P. floridanus* and *L. truncatellus*. However, sufficient evidence is available to show that as the number of embryos per egg increases the polyembryonic process becomes more and more complicated. A comparison of the development of *P. vernalis* with that of *C. gelechiae* shows that each true germ of the former develops directly into an embryo, usually without division, while in the latter each multinucleated morula of the late polygerm stage always divides to give rise to two morulas, and hence to two embryos (Leiby, '22). Moreover, during the formation of the polygerm of *C. gelechiae*, there is an extensive multiplication of the embryonic nuclei before the primary germs are organized, and when they are formed, by groupings of these nuclei, their number is comparatively large. This, together with the fact that each morula divides to produce two embryos, accounts for the greater number of embryos arising from the egg of *C. gelechiae*.

In *Paracopidosomopsis* the polyembryonic process is even more complicated than in *C. gelechiae*, but Leiby and Hill ('23) who have also examined this species, believe that the secondary morulas divide to form tertiary morulas which then differentiate into larvae.

In this brief review of the development of the complex types many of the details have necessarily been omitted, but it is hoped that sufficient have been given to indicate to the reader the course of polyembryony in the Hymenoptera.

5. QUADRUPLETS IN THE TEXAS ARMADILLO

In two species of the armadillo there occurs a form of polyembryony which is regarded by some as a modified type of twinning. The two species concerned are the Texas nine-banded armadillo, *Dasypus (Tatusia) novemcinctus*, and the South American Mulita, *D. hybridus*. The Texas armadillo typically produces four identical quadruplets from a single egg, while the

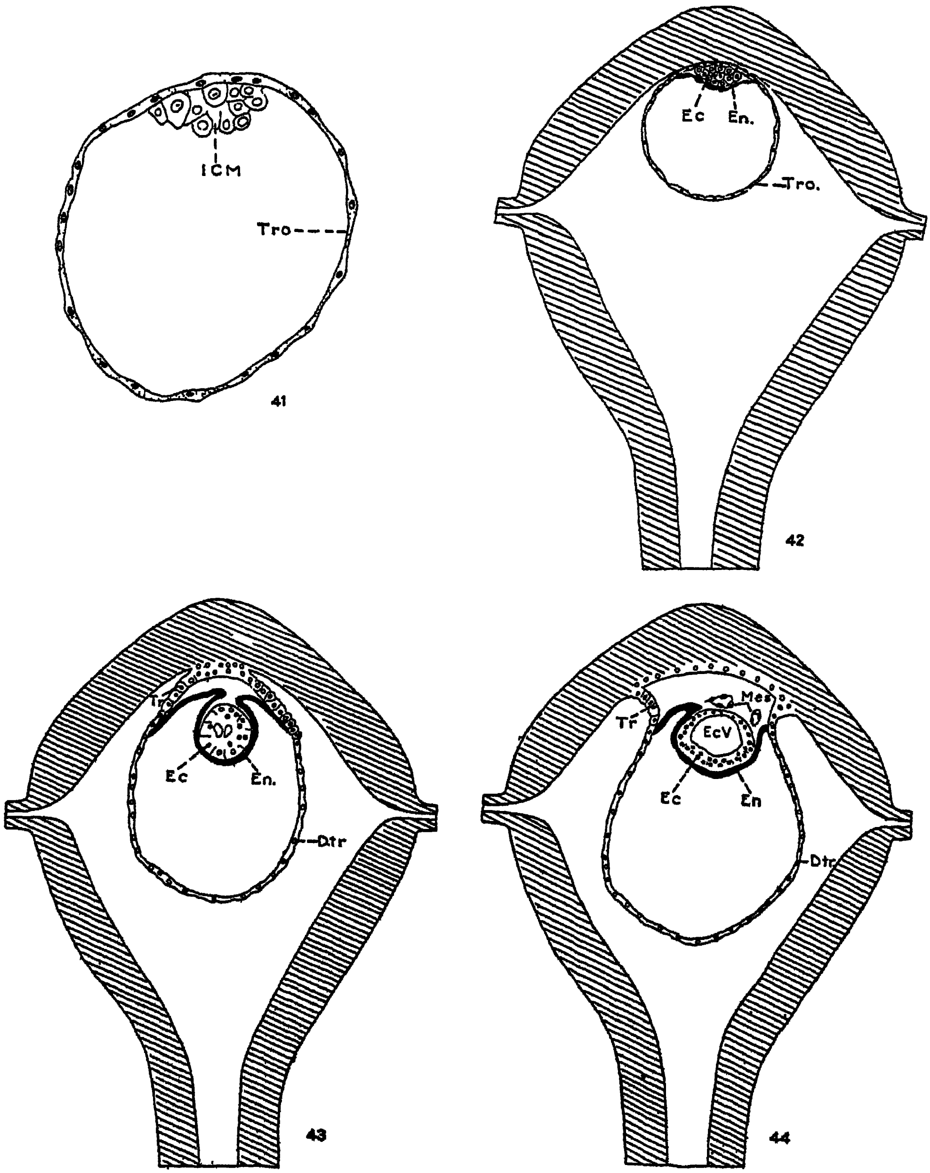
egg of Mulita gives rise to from seven to twelve individuals. In each species the several individuals arising from one egg are of the same sex.

H. von Ihering ('85, '86) was apparently the first to suspect that all of the young of one litter might be the product of one egg, for he had observed in each of two pregnant females that the eight embryos present were inclosed in a single chorion, and that all of the fetuses were of the same sex. However, the real discovery of polyembryony was not made until 1909. During that year two papers appeared in which it was shown that the several fetuses found in the pregnant uterus of each of the two armadillos are derived from one egg. Fernandez ('09), on the basis of his observations on several stages of Mulita, concluded that it was a case of polyembryony, and Newman and Patterson ('09) working on a few advanced stages of the Texas species, concluded that the four embryos must come from a single fertilized egg. Following this, a number of papers on the subject were published by Newman and Patterson, both in collaboration and separately, on the Texas armadillo, and by Fernandez on Mulita. As a result of these investigations it has been conclusively demonstrated that the mode of development is that of polyembryony, and that the process is practically identical in the two species. The following brief account is based chiefly on the conditions found in the Texas armadillos.

Unfortunately, the early cleavage stages of the armadillo ovum have never been secured for either species, but in the Texas species a series of developmental stages extending from late cleavage to full term, has been obtained and studied (Patterson, '13). The youngest ovum available has already passed through the so-called morula stage, and has become an embryonic vesicle or monodermic blastocyst. Such vesicles are usually found free in the cavity of the uterus, although a very few have been washed out of the fallopian tubes. We now know that the armadillo breeds sometime before the 15th of August, for a female of breeding age usually has a free vesicle in the uterus by that date. (For this datum I am indebted to Mr. G. W. D. Hamlett of this laboratory. Mr. Hamlett has made an extensive study of the breeding habits of the armadillo, and has secured a very large series of free vesicles and other early stages.) The remarkable fact is that the vesicle does not become permanently attached to the uterine mucosa for several weeks, or until sometime in October or November. A similar "period of quiescence" has also been reported for the blastocyst of the deer (Bischoff).

The young blastocyst of the armadillo is similar in practically every respect to that of many other mammals, and its structures give no evidence that it will produce four embryos instead of one. The blastocyst is composed of a typical trophoblastic layer, and the usual group of embryonic cells, or inner-cell mass (fig. 41). During the period in which the blastocyst is free in the uterine cavity, the inner-cell mass becomes differentiated into the two embryonic layers, the ectoderm and entoderm.

The didermic blastocyst then becomes attached to the mucosa at the tip of the fundus end of the uterus, on an area of the mucosa known as the attachment zone. The area of the trophoblast that forms the seat of attachment is the portion which directly overlies the embryonic ectoderm, and which is called Rauber's layer. Sometime before, the ovum, which is in the form of a flat, circular



FIGS. 41–44. FOUR STAGES IN THE DEVELOPMENT OF THE ARMADILLO BLASTOCYST

In figs. 42–46 the blastocyst is represented in a section, which is placed in a diagrammatic section of the uterus. In order to save space, the size of the diagram of the uterus is made much smaller in proportion to the size of the blastocyst. Fig. 41. A section of a very young blastocyst, showing the single layered trophoblast and the inner cell mass (I.C.M.). For a description of figs. 42–44, see text.

plate, becomes distinctly thicker (fig. 42), and after attachment it is gradually transformed into a spherical or ball-like mass. The primary entoderm does not completely line the inner surface of the trophoblastic wall as in some mammals,

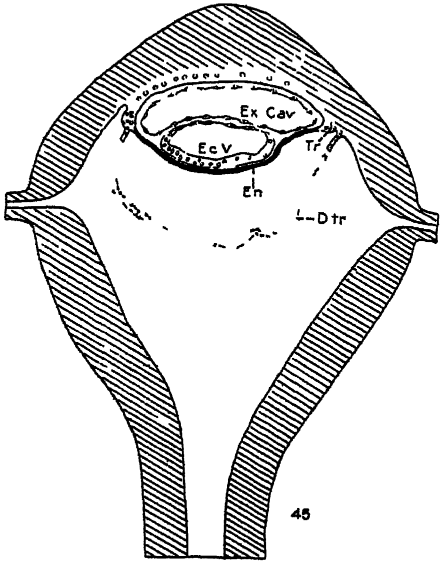
but its free edge ends a short distance beyond the limits of the ectodermal mass (fig. 42, *En*). This free edge becomes attached to the trophoblast, forming a zone which extends around the ectodermal sphere. The attached edge forms the pivot upon which the entoderm turns during the so-called process of germ-layer inversion. Shortly after the ovum becomes attached, the spherical mass of embryonic ectoderm leaves the inner surface of the trophoblast and moves downward, carrying before it the layer of entoderm. The entoderm finally all but completely envelops the ectodermal mass (fig. 43). The trophoblast becomes differentiated into two distinct regions. First, that portion which directly overlies the ectoderm thickens and forms an intimate union with the mucosa. It is recognized as the trophodermic region, and upon further development forms the primitive placenta, or Träger (fig. 43, *Tr*). The rest of the trophoblast, which lies beyond the edge of the entoderm, undergoes no striking morphological changes. It is the diplotrophoblast.

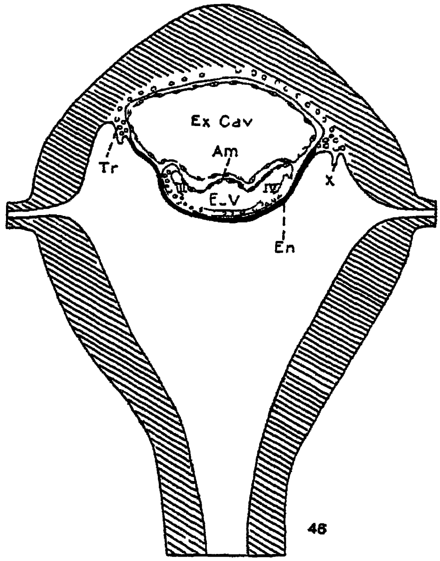
The ectodermal sphere is soon changed into a vesicle. The first evidence of this is seen in the appearance of vacuoles, lying toward the center of the sphere (fig. 43). These coalesce and transform the solid sphere into the ectodermal vesicle (fig. 44, *Ec.V.*). The cavity of this vesicle is the common amniotic cavity of the later stages. The movement of the ectodermal sphere away from the trophoderm creates a cavity between the sphere and the trophoderm. Groups of cells, apparently arising from the upper portions of the ectoderm, invade this space and soon form small vesicles. These constitute the beginning of the extra-embryonic mesoderm (fig. 44, *Mes*). The mesodermal vesicles fuse together and eventually form a complete living membrane for the extra-embryonic cavity (fig. 45, *Ex.Cav.*).

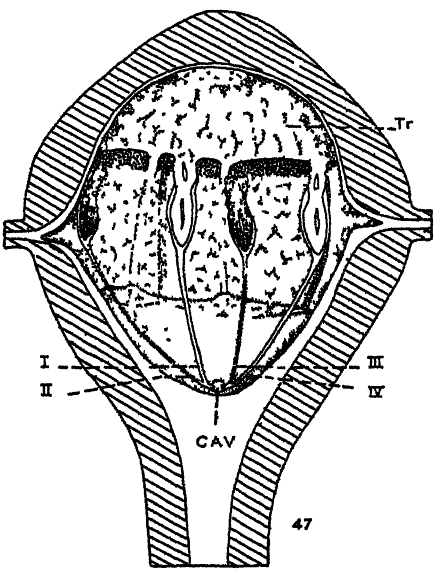
It is about at this stage (fig. 44) that the first evidence of polyembryony becomes apparent. At first the wall of the ectodermal vesicle is equally thick on all sides, but there follows a shifting of cells in such a way that the upper side of the vesicle gradually becomes thinned out (figs. 44, 45). This upper portion constitutes the true amniotic layer of ectoderm, while the lower or thicker portion represents the true embryonic ectoderm. The first evidence of the embryonic rudiments is seen in the appearance of the two blunt diverticula, extending out laterally from the opposite sides of the ectodermal vesicle. In the original publication (Patterson, '13) these were designated the primary buds. A median longitudinal section passing through the two primary diverticula is seen in figure 45. These diverticula lie on the right and left sides of the ectodermal vesicle. The embryonic ectoderm extends out into the diverticula as thick plates. The diplotrophoblast (fig. 45, *D. tr.*) has usually disappeared by this time, and in the figure is represented by a broken outline. The disappearance of the diplotrophoblast directly exposes the yolk sac entoderm to the uterine cavity.

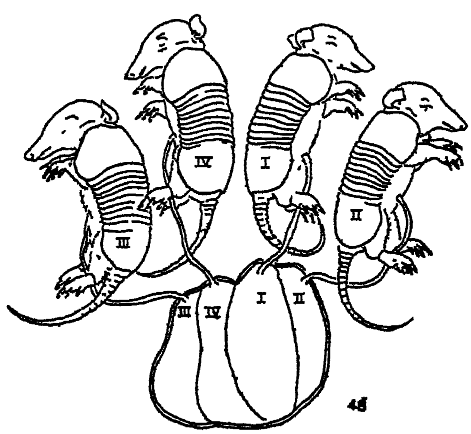
The next step in the formation of the quadruplets in the armadillo blastocyst consists in the division of each primary bud to form two secondary buds. Consequently, there are in all four embryonic rudiments. The secondary diverticula arise in each primary as two thickenings in its wall. One of these is situated at the extreme tip of the primary bud, while the other appears slightly to the left (as viewed from the yolk-sac of each of the blastocysts). The Roman numerals I to IV, are used to designate the four primordia thus produced. The embryos

are, therefore, grouped in two pairs, Nos. I and II constituting one pair and Nos. III and IV the other pair. To distinguish this fundamental arrangement of the embryos from that of their final position in the uterus we shall refer to it as the primary pairing.









Figs 45–48 See text for description of figs. 45–46. In fig. 47 the entire blastocyst is shown in the diagram of the uterus The relative sizes of uterus and blastocyst are approximately that of normal. Fig. 48 shows uterus split open and the four half-grown fetuses spread out in such a way as to reveal their paired arrangement.

In figure 46 is shown a section passing through the embryonic rudiments II and IV. The diverticula of these two embryos

extend out laterally from the right (IV) and left (II) sides of the original ectodermal vesicle (*Ec. V.*), from which they are slightly constricted. The yolk sac entoderm is now directly exposed to the uterine cavity, due to the fact that the diplotrophoblast has entirely disappeared. That portion of the entoderm upon which the embryonic ectoderm of each embryo comes in contact will form the gut entoderm for the embryo. The ventral sides of the embryos, therefore, face the uterine cavity. The anterior or head ends of the embryos all point toward the apex of the common ectodermic vesicle, or what may now be called the common amniotic vesicle.

In the subsequent development of the blastocyst and its embryos, there occurs first a very rapid growth of the Träger region, so that the egg extends down farther and farther into the uterine cavity. At the same time the embryonic rudiments retreat from the amniotic vesicle toward the rim of the advancing Träger region. Eventually, the posterior end of each embryo unites with this rim. It is from this point of union that the umbilicus later arises.

The embryo in thus moving away from the ectodermal vesicle, draws the amniotic ectoderm out into a long, slender tube, the connecting amniotic canal. The original ectodermal vesicle, from which the embryonic rudiments arose, is left, as the common amniotic vesicle, at the lower apex of the egg.

The relationship of the embryos to the various parts of the egg is brought out in figure 47. The egg is represented as a semi-transparent object, placed in a diagrammatic section of the uterus. Each embryo has reached the primitive streak stage, and has its anterior or head end directed toward the common amniotic vesicle, with which it is connected by a canal. Its posterior end is united with the rim of the Träger. The four connecting canals converge toward the amniotic vesicle. It will be noted that the four canals do not enter the vesicle at separate points, but those from embryos I and II first unite and then enter the vesicle as a single tube. The canals from Embryos III and IV enter in a similar manner. This relationship indicates the primary pairing of the four embryos.

Villi are beginning to appear on the Träger area (fig. 47, *Tr.*). In early somite stages this region is thickly covered with simple villi, with the exception of the upper tip end, which is practically free from these structures. In stages in which the embryos have reached a head-rump length of from 12 to 15 mm., the placenta consists of four more or less distinct discs, each covered with branching villi. The placental discs occupy a position slightly above (toward the fundus end) of the chorionic vesicle. In the advanced stages of development, these discs are distinctly paired, one pair occupying approximately the left side and the other the right side of the vesicle. The villi of the upper part of the vesicle remain practically undeveloped, so that this area of the Träger becomes non-placental. As the chorionic vesicle develops, its lower yolk-sac end becomes relatively smaller and smaller, until in the late stages of gestation it constitutes only a small, clear, cap-like area at the lower apex of the vesicle.

In the final stages of gestation the cavity of the chorionic vesicle becomes divided into four quadrants, partitioned off by the amnia of the four fetuses. Each quadrant contains a fetus and its umbilicus. The arrangement is such that embryo No. I occupies the ventral quadrant and its paired mate (II) the left quadrant, while embryo No. III occupies the dorsal quadrant and its mate (IV) the right quadrant.

This arrangement clearly constitutes a secondary pairing, which may or may not correspond to the primary pairing, for it is possible to demonstrate, by a study of early budding stages, that the four embryonic diverticula do not necessarily show the same relation to the uterine axes as do the four fetuses of the late stages. (The facts upon which this statement is based are contained in an unpublished manuscript.) In certain cases the two primary diverticula, instead of extending out from the right and left sides of the ectodermal vesicle, grow out from the dorsal and ventral sides, respectively. Hence, the secondary diverticula of either primary bud will extend to the right and left sides of the dorsoventral plane of the uterus. Since all traces of the primary pairing disappear at a comparatively early stage of development, when the common amnion and its canals degenerate, it is never possible to tell whether or not the secondary pairing is the same as the primary. It may well be that when the primary buds arise from the dorsal and ventral sides of the vesicle embryos I and IV will constitute one of the secondary pairs, and Nos. II and III the other pair. The lateral arrangement of the paired discoid placentae, lying as they do on the right and left sides of the chorionic vesicle, must be regarded as the result of the bilateral blood supply of the uterus, rather than the result of the primary pairing of the embryos.

6. DISCUSSION

A general survey of the subject of polyembryony makes it clear that this type of development has arisen independently in several different groups of animals, and in some of these groups has undergone a distinct evolution. Since polyembryony has thus arisen and evolved it is not to be expected that its exact mode of expression would be the same in each of the several groups in which it is found. For this reason, any attempt to apply a general theory as to the cause of polyembryony is certain to meet with difficulties. Nevertheless, it is possible that in the final analysis it will be found that the causal factors underlying the production of multiple embryos are the same in all cases, irrespective of the exact mode of origin or the number of embryos arising from the egg.

Various theories have been advanced to explain the occurrence of polyembryony, such, for example, as the "blastotomy theory," the "fission theory," the "budding theory," and the "physiological isolation theory." While some of these theories may have merit, yet I think that no one of them is adequate to account for the origin and development of polyembryony among the different animal groups. The various theories have been discussed rather fully by Newman ('17, '23), Stockard ('21), and the writer ('13), and need not be reviewed in this brief discussion. Instead, I shall consider certain facts of polyembryony that may bear on the question of theory.

In discussions on the subject of polyembryony it has not been customary to emphasize the obvious fact that specific polyembryony is a developmental characteristic which is definitely inherited, and as such it must arise and become incorporated in the hereditary mechanism in a manner similar to that of any other heritable character. That is to say, it must arise as a variation having survival value, and hence effective in adaptation. Specific polyembryony can be interpreted as a form of adaptation, for the reason that it results in an increase in the number of offspring from the egg. This might

have the effect of increasing the chances of survival of any species having this type of development.

There is considerable evidence to show that polyembryonic development has undergone a very distinct evolution within certain groups, *e.g.*, the parasitic Hymenoptera. In the Hymenoptera it is possible to arrange a series in which polyembryony begins as a simple type of twinning, and gradually increases in complexity until in some species more than a thousand individuals are produced from one egg. Moreover, it is possible to trace throughout this series the several steps by which this complexity has taken place.

The same is probably true for the armadillos, although the evidence is less complete. The facts on the development of armadillos are still fragmentary, but such as we have clearly indicate that the armadillos were formerly multiparous, and then gradually evolved to a condition of uniparity. In the living species the uterus is of the simplex type, somewhat like that of the human. Nevertheless, some of the non-polyembryonic species still show a strong tendency to ovulate and gestate two eggs. Some few species, however, are said to be entirely uniparous. It is from this condition that polyembryony has evolved; first by the production of identical twins (probably), then by the formation of quadruplets, and finally by the production of from eight to twelve embryos from the egg.

Another point of significance is the fact that before specific polyembryony is established in a given group of organisms the monembryonic type of development in the group often has become highly specialized, and it is probably true that without such specialization polyembryony would not become established as the exclusive mode of development.

This review has been devoted almost entirely to cases of specific polyembryony, but in conclusion it seems desirable to make a suggestion concerning what has been termed sporadic polyembryony. Such cases occur throughout the entire animal kingdom, although their appearance in any given species may be very rare. In some species sporadic polyembryony gives every evidence of being hereditary. Thus in the case of human identical twins several writers have pointed out that such twinning must be inherited, because of the fact that it appears with very great frequency in certain families (see Davenport, '20). However, most cases of sporadic polyembryony give no evidence that heredity is involved. From reading the reports on such cases, one gains the conviction that their occurrence is the result of "environmental accidents," such as the separation of the early blastomeres. I would suggest that the results obtained in experimental polyembryony offer an explanation of the cause of such sporadic cases rather than that of specific polyembryony.

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ABNORMAL SEXUALITY IN ANIMALS

III. SEX REVERSAL

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IT IS somewhat difficult, when one first approaches this subject of the transformation of sex, to grant that reversal is possible in the higher forms in which the sexual differences, morphological, physiological, and mental, are so sharply emphasized. But when one remembers that what is rare and exceptional in one form can be facultative in others, and that all forms have much in common, the difficulty vanishes. It is readily conceded that the oyster, for example, may regularly change its sex. The native oyster begins its life as a male and then, when one or two years old, may and indeed commonly does become a female. But that is not all, for Orton (1921) has shown that such an oyster, after becoming "white sick," *i.e.*, after shedding its ova into the mantle cavity, and whilst still carrying its own embryos, can, within the space of a month, become equipped as a male once more. That which is usual in the oyster may be under certain conditions not rare in the more highly organised forms. Similar instances of facultative sex-transformation are those furnished by *Crepidula plana* (Conklin, 1898; Orton, 1909; Gould, 1917), parasitized Cymotheids and Epicarids (Mayer, 1879; Caullery, 1908; Bonnier, 1900; Smith, 1906), *Asterina gibbosa* (Cuénot, 1898; Harms, 1926), and *Limax maximus* (Baber, 1894). In all these cases the direction of the transformation is ♂–⚥–♀.

The sex of an individual of a bisexual species is said to have been completely reversed when the individual has assumed the sex-characterization typical of one with the alternative sex-chromosome constitution. Thus sex-reversal of a female implies that a genotypic female (XX) loses her typically female sex-characterization and develops that type of sex-equipment which is essential for the elaboration of functional spermatozoa and for the efficient conveyance of these to the site of fertilization.

The recorded instances of this phenomenon occurring in species in which it is to be regarded as abnormal can be classified for purposes of discussion according to the following scheme.

A. Sex-reversal can be the direct expression of genetic action

If the genetic components of sex-reversal are present in the genotype of an individual, if the physiological equilibrium of the zygote established by the action of the genotype (the sum total of all the genes) is not profoundly modified by the physiological influence of the glands of internal secretion during development, and if the impress of external agencies upon the zygotes does not or cannot override the genotype, *i.e.*, does not or cannot profoundly alter the physiological state established by the genotype, then sex-transformation will occur as development and differentiation proceed.

Thus in the case of the moth, *Lymantria*, and similarly constituted forms, the forces which lead to intersexuality lead also to sex-reversal. Intersexuality is in such cases merely incomplete reversal. Complete reversal will occur when in a genotypic male the quantitative disharmony between the male and the female sex-differentiating reactions is such that the female reactions are in excess throughout the whole of the period of differentiation, or in the case of a genotypic female when the male reactions are in efficient excess throughout this time.

In the Lepidoptera Goldschmidt (1920, 1923), Harrison (1919), and others, have obtained species hybrid broods that were largely or entirely of one sex. Harrison was able to show that in one of his cases the mortality was not sufficiently high to account for the results obtained; it was not a case of a sexually selective prenatal mortality, and both Goldschmidt and Harrison have presented evidence which strongly indicates that the results are due to a sex-transformation of half the individuals concerned. Unisexual broods in these forms are to be regarded as the final stage of intersexuality. Sturtevant (1920) records similar unisexual broods in *Drosophila melanogaster* × *D. simulans* crosses, but finds that the cause of this is a selective mortality.

Another instance of direct genetic sex-reversal would seem to be that of the fish *Xiphophorus*. Essenberg (1925) records that sex-reversal occurs in the viviparous teleost fish, *Xiphophorus helleri*, (the sword-tailed minnow), and that many instances of this have been reported by fish breeders and fanciers. In Essenberg's cases two females ceased to produce young when about three years old, and during the course of several weeks took on the sex-characters of the male. Cytological examination revealed the presence of ripe sperm in all parts of the gonad which, however, was juvenile in relation to the size and age of the fish. Essenberg was able to show that there is a type of development in the female which readily provides a morphological basis for the change-over. He also shows that there is a complete reversal of the sex-ratio in a population, this being 50:100 among immature fish and 100:50 among mature, a fact which supports the suggestion of sex-transformation of 50 per cent of the females. In many males, moreover, the shape of the testes closely resembles that of the ovaries, and the grades suggest a transformation of pre-existing ovary into testis. It would seem from Essenberg's observations that sex-reversal is extremely common in this fish and that it is genetic in origin, there being a form which through genetic action is destined merely to pass through a female phase and later to proceed to a male type of sex-differentiation. The case is very similar to that of *Lymantria*, save that even in a well grown individual a remodelling of the sex-organization can take place, there being no permanent hard parts.

Harms (1926) also has observed the transformation of females of *Xiphophorus* into males at different ages, especially among old sterile females. He records that during this process of sex-reversal the female when mated still produces young, though when the process is completed, the individual is a functional male, larger than the normal male, broader and heavier. Harms observed that the older the animal is at the time of the change-over, the more female the general body build remains. The process occupies about 3–4 months and in the case of old females it may remain incomplete. The cause of the transformation is regarded by Harms as being a physiological exhaustion of the ovary with a consequent alteration

in the general metabolism which invokes the differentiation of testicular tissue. He thinks that inbreeding favors sex-transformation.

Harms bred from his transformed females when they were functioning as males and got none but females, as would be expected if the female of the fish is monogametic and if sex-reversal does not affect the nature and distribution of the elements of the sex-chromosome sex-determining mechanism.

Other cases of what would seem to be sex-reversal in fishes have been recorded by Herzenstein (quoted by Essenberg) in the cyprinodonts *Cymnocipris potanini* and *Schizopygopsis güntheri*, in which cases also females assumed the sexual characters of the male. Philippi (1904) reported a similar case in the viviparous teleost, *Glaridichthys caudimaculatus*, and three others in *Glaridichthys januarius*, while Newman (1908) described a case of hermaphroditism in *Fundulus majalis* which would seem to be one of sex-reversal. Winge (1927) describes certain cases of intersexuality in *Lebistes reticulatus* which may possibly be of this nature. The changes occurred in old females which though still functioning as females assumed certain of the male sex-characters.

A very considerable number of cases of hermaphroditism in different species of fish have been recorded. It is unfortunate that in the majority of these the description is inadequate; however, the indications described are either stages in sex-reversal or are cases of intersexuality similar to those occurring in the mammal. That certain of them are indications of a sex-reversal probably exactly similar to that in the case of *Lymantria* is very probable. In addition to the case of *Xiphophorus* there is the suggestive one of *Girardinus poeciloides*, the "millions" fish, examined by Huxley (1920). Boulenger had reported that the sex-ratio of a stock bred in the London Zoological Gardens was three females to one male for a period of nine to ten months, that this had then given place to a sex-ratio of one female to two males, and lastly to one of equality. Huxley suggests that this swing in the sex-ratio is due to the fact that some of the females of the population in which the sex-ratio was three females to one male were genotypic males which had undergone sex-reversal to become phenotypic (or somatic, as Shull, 1914, would call them) females. These phenotypic females, still XY in sex-chromosome constitution, would elaborate two sorts of eggs, in respect of the elements of the sex-determining mechanism, instead of one, and these being fertilized by X- and Y-bearing sperm would yield in every three on the average one female (XX) to two males (XY), the YY zygote being non-viable. If this sex-reversal had affected a certain proportion of the males of one generation, then two out of every three females would be normal in the next, so that the sex-ratio would swing back to five females to six males. If sex-reversal continued for several generations there would ultimately be a swing in the opposite direction to give a preponderance of males.

Langerhans (1876), Goodrich (1912), and Orton (1914), have recorded cases of intersexuality in *Amphioxus*. Orton's specimen was 4.4 cms. long and was predominantly male; only one of the forty-three gonad pouches contained ova, the rest being filled with sperm. The digestive gland was also abnormal. Orton suggests that these cases are but stages in a process of sex-transformation in the direction male-female. These intersexual specimens were of medium size.

It will be noted that the interpretation offered later on to explain sex-transformation in the fowl suggests that in the bird

also the genetic components of sex-reversal are present in every hen. In effect, it is suggested that every hen would inevitably become a cock but for the fact that within her body there is an ovary, a legacy from the phase of her development when the valency of the female determining reactions was greater than that of the male reactions. It is the physiological influence of the ovary which prevents the expression of the genotype: if the ovary is removed, then an internal environment of maleness, the direct expression of the genotype after embryonic life, becomes established, and a male characterization is assumed. But since the ovary remains in the "normal" hen, sex-reversal is abnormal; it occurs only when the genotype is unbolted by the removal of the ovary. For reasons of convenience, the case of the fowl is not included in this category to which indeed it would seem to belong.

B. Sex-reversal can be the result of the overriding of the genotype by agencies which sufficiently disturb the general physiological conditions of the zygote at some stage or other of its development

1. It can result from a disturbance of the physiological condition within the ovum before fertilization. The work of Hertwig (1906, 1912), of Kushakevitch (1910), and of Witschi (1914), has shown that delayed fertilization and also the exposure of the eggs before fertilization to high temperature (27°C.) leads to a profound disturbance of the sex-ratio among the offspring. The male frog was permitted to fertilize half the eggs of a female and then was removed, to be replaced after an interval to fertilize the remaining eggs. After an interval of 89 hours none but male offspring were obtained. It was established that this result was not due to selective fertilization, to a sexually selective mortality among the embryos, or to the abnormal extrusion of the X-chromosome during the maturation of the ova. The correct interpretation of the results would seem to be that some 50 per cent of the eggs were fertilized by X-chromosome-bearing spermatozoa, genotypic females (XX) being produced, but that the conditions of the experimentation were such as to transform these into phenotypic males, the sex-chromosome constitution of the zygote being overriden by the effects of delayed fertilization upon the metabolism of the egg. The results obtained by Mršić on the effect of overripeness upon the egg of the trout are probably to be explained in a similar fashion.

King (1912) has shown that desiccation of the toad's egg yields exactly opposite results, for she obtained 87 per cent of females in an experiment in which the mortality among individuals of unknown sex was less than 7 per cent. In the case of the frog, Witschi (1914) not only obtained individuals which were instances of complete sex-reversal but got in addition numerous intersexual forms of various grades.

The observations of Adler (1920), who has shown that the thyroids of individuals from these late fertilized eggs are markedly hypertrophied, would seem to be of significance. Adler suggests that in these individuals the thyroid comes into action earlier than does the gonad and so affects the internal environment that the gonads, when they do differentiate, become testes.

These observations are closely in line with those of Whitman (1919) and of Riddle (1912, 1916) upon the pigeon. It was found by Whitman that the matings of birds belonging to the Columbidae and of two widely different zoological families resulted in the production of male offspring only, and that female offspring alone were obtained from the eggs of

doves which had been forced to lay excessively and at an abnormally rapid rate. Riddle carried these observations further and was able to show that the eggs that yield males can be distinguished from those which yield females, that maleness is associated with eggs of smaller size, higher water content, and less stored energy, and that the production of all males or of all females was associated with the production of eggs of one or of the other type. He was able to dismiss the possibility of selective fertilization and of differential maturation, and was driven, against his will it would seem, to the conclusion that the conditions of the experiments were such as to induce sex-reversal in the egg itself (1914, 1919).

It is a simple matter to interpret these results in terms of a metabolic theory of sex as elaborated by Riddle. Delayed fertilization implies an increased metabolic rate in the egg and a high metabolic rate implies maleness. Desiccation implies a decreased metabolic rate and femaleness. The hypertrophy of the thyroid implies an increased metabolism and an internal environment of maleness. The production of offspring all of one sex by matings of wide crosses is to be interpreted as the result of the pooling of genes which in their action lead to the establishment of one kind or the other of metabolic level in the zygote. Castle (1926) discussing the general question of hybrid vigor argues that the zygote is not a mere summation of the factors contained in the two gametes but that the hybrid state itself is a source of metabolic energy in the zygote. There seems, however, no real difficulty in assuming that the ultimate source of metabolic energy is the genotype.

In this connection it is of interest to note that Guyer (1909) has collected data on species hybrids among certain birds and has shown that there is a decided excess of males in the F_1 generation. The cause of this has not been demonstrated. Riddle (1916) recorded an excess of females in the cross *Streptopelia risoria* × *S. alba* (doves) under certain conditions and concluded that this excess was the result of a transformation of some of the males. It has been shown, however, that this conclusion is not justified, for the cross involved a sex-linked character and of the hybrids the males are dark, the females white in color, and examination of the data for sex and also for color shows that the only possible explanation of the excess of females is that which postulates that the conditions of the experiment were such as to cause the X-chromosome to pass into a polar body at the time of the reduction divisions more often than to remain in the egg.

Riddle (1912, 1914, 1916, 1917) has shown that a higher metabolic rate is associated with maleness and a lower rate with femaleness. He has shown that in the case of his pigeons the season of the highest male production is the winter and that is the season when the thyroid of the pigeon is largest and when there is least storage of energy within the ova, as estimated by burning the yolk in a bomb calorimeter; and conversely that the period of the greatest energy of fat storage and of the smallest thyroid size is the period of the greatest excess of females, and he argues that the facts concerning the type of metabolism induced by the different kinds of experimentation all point to the conclusion that the causal agent in sex-transformation is the establishment of that type of metabolism which is characteristic of the alternative sex. It may be that many of the peculiar phenomena associated with parthenogenesis, particularly those which concern the effect upon the sexuality of the egg of environmental

agencies (Maupas, 1891; Banta and Brown, 1924) are to be explained in a fashion somewhat similar to the above.

2. *It can result from a disturbance of the general physiology of the individual during embryonic life.* It is possible, but not probable, that those agencies which commonly lead to the production of a free-martin in cattle and goats occasionally result in the production of a completely transformed individual (Lillie, 1923; Bissonette, 1924). This, however, must yet awhile remain pure speculation.

Burns (1925) joined young embryos of *Amblystoma* in the tailbud stage in parabiosis and instead of getting the expected chance combinations of the sexes, 1 ♂♂, 1 ♂♀, 1 ♀♂, 1 ♀♀, he obtained exclusively one sexed pairs. He suggested that the reason for this 44 ♂♂: 36 ♀♀ or 1:1 ratio was that in one-half of the original ♂♀ and ♀♂ associations the males became transformed into females, whereas in the other half the females became transformed into males.

Witschi (1927), using four different species of frogs, joined embryos 50–70 hours old, and shortly after the closure of the medullary tube, in parabiosis. The controls exhibited the first signs of sex-differentiation during the third week of development; in the case of the parabiotic twins it was somewhat delayed. The twins were preserved at intervals during the larval period and the stage of metamorphosis. The sex-ratio among the controls was 96 ♂♂ : 100 ♀♀ or 1 : 1. Among the 56 twins there would be expected the following sex-combinations: 14 ♂♂, 14 ♂♀, 14 ♀♂, 14 ♀♀. There was found on examination 16 ♂♂, 17 ♂♀ (with 7 of the ♀♀ exhibiting some stage in sex-reversal), 10 ♀♂ (with 4 of the ♀♀ undergoing sex-reversal), 13 ♀♀. The combination of a female with a male twin undergoing sex-reversal was not encountered. Witschi therefore concluded, unlike Burns, that the male sex-differentiating agencies predominated and that sex-reversal did not take place before the time of sex-differentiation since 29 one-sexed and 27 two-sexed pairs is as near as possible to the expected 28 $\pm$ 2.5 and among the individuals there were 59 ♂♂ and 53 ♀♀, the deviation from the mean being less than the single P.E.

Disharmonies in the time relationship during development when the stimulus to sex-differentiation is exhibited may provide opportunity for sex-reversal. For example, in *Myxine* (Schreiner, 1904), growth would seem to proceed undirected to the stage when the individual is hermaphroditic, before the processes of sex-differentiation set in to convert the individual either into a functional male or else into a functional female. In the young males of *Perla marginata* both ovarian and testicular tissues are to be found but the ovarian tissue undergoes atrophy, so that in the adult none but testicular remains (Junker, 1923). In such circumstances as these the morphological basis of a possible sex-reversal is revealed and it becomes entirely conceivable how physiological disturbances during embryonic and early post-embryonic life can change the course of differentiation and lead to the conversion of a genetic male into a functional female, and *vice versa.*

In his interpretation of the bovine free-martin, a female rendered abnormal in respect of her sex-organization by the action of the physiological influence of the testes of the male co-twin *in utero* which enters her body by way of a vascular anastomosis, Lillie rejects the idea of the dominance of the male sex-differentiating reactions in favor of a time relation in the production of male and female hormones, that of the testis, as suggested by the work of Chapin (1917) and of Bascom

(1923), being elaborated earlier in development. Lillie, however, freely admits that other causes may also exist. In the case of the parabiotic twins of frogs the time factor does not enter, for there is a physical basis for a definite antagonism between male and female differentiators. The male differentiating reactions first embarrass and then suppress the female.

Doncaster (1920) suggested that the occasional tortoiseshell male cat was a sex-reversal female produced in the same way as is the free-martin in cattle. He, and later Bamber (1922), examined a considerable number of pregnant uteri of cats and found no instance of a confluence of blood vessels. Bamber (1922) puts forward the suggestion that the tortoiseshell male is indeed a transformed female or *vice versa*, but that the reversal is not the result of the intra-uterine action of the sex-hormone of a male co-twin but of a metabolic change in the egg similar to that described by Riddle in the case of his pigeons. In a later paper (1927) however, she exhibits a preference for another interpretation.

3. It can result from a disturbance of the general physiology of the post-embryonic individual. The conditions necessary for such sex-transformation are (1) there must be a switch-over from one type of metabolism to the other, from the female to the male, or *vice versa;* (2) the component structures of the sex-equipment must be capable of transformation or replacement, one kind of gonadic tissue must be replaced by the other, ovary must become or be replaced by testis, or *vice versa*, the accessory sexual apparatus, the external organ of reproduction, the rest of the secondary gonadic characters must be remodelled or replaced.

Complete sex-reversal therefore cannot occur in any individual or form in which the internal and external genitalia, being fashioned early in embryonic life, thereafter lose their plasticity and become unresponsive to any stimulus which, had it been exhibited at the time of their differentiation, would have controlled these processes. Nor can it occur in those cases in which the differences between male and female sex-equipments are based upon the differential development of two different sets of structures one of which, in either sex, undergoes complete atrophy. No more can it take place in those forms in which sex-dimorphism involves a differential mode of development of one and the same set of structures, for if one plan of differentiation is pursued, the steps cannot be retraced and the alternative route then followed.

Harms (1923) and Guyénot and Ponse (1923, 1925) have shown that if young castrated male toads are fed on a diet containing an excess of fat, lipoids, and lecithin for a considerable period of time, the caudal portion of Bidder's organ becomes differentiated as an ovary and the cephalic portion as a new organ of Bidder, and that oviducts and uteri are developed while the pointed head becomes transformed into the blunted characteristic of the female. Ponse (1925) succeeded in rearing 9 metamorphosed offspring of one such transformed male functioning as a female and of these 6 were males and 3 females. Harms raised 184 such offspring and of the 161 the sex of which could be identified there were 104 males and 57 females. If in the toad the male is digametic, and if the YY zygote is non-viable, the expected sex-ratio is 2 ♂♂ : 1 ♀.

In this connection reference must be made to the work of Russo (1911), who recorded that in the rabbit there are two kinds of fertilized ova, one containing lecithin and the other crystals of fatty acid. He suggested that the lecithin-containing ova are anabolic (female),

the others catabolic (male). The experiments of Russo (1909) in which he endeavored to affect the sex-ratio by administering lecithin have been subjected to severe criticism by Basile (1908), Punnett (1909), and Castle (1910). However, there would still seem to be reason for holding that Russo's work should again be repeated.

Champy (1921) records that when a male triton (*T. alpestris* Laur.) was fed intensively after the winter's starvation, he assumed the external characters of a female, and that within the pre-existing testicular tissue there were to be found immature but unquestionable ova. He had previously shown that the annual process of spermatogenesis in tritons could be inhibited by starvation and that in the absence of spermatogenesis there was no development of the external sexual characters, the animal exhibiting the "neuter" state corresponding to that of the male in winter. In this "neuter" state there are to be found in the testes primitive gonocytes and spermatogonia. In animals killed in the spring, following starvation, the testis was represented by a longitudinal strip of fat. Two of these starved "neuter" tritons, when fed intensively, lost the dark blue even coloration of the back and assumed a greenish shade mottled with distinct blue marks, as in the female, whilst the yellow dorsal line became more and more attenuated. One of these animals was killed in January and there was found the expected strip of fat with a few spermatogonia. The other was kept alive and in February was exactly like a female in appearance. It was kept until April when post-mortem examination revealed within each of the strips of fat an elongated organ of granular appearance resembling an ovary, together with an oviduct.

Histologically this organ was an immature ovary. Champy points out how this case exemplifies the ambivalency of the primitive gonocytes for these, instead of becoming sperm, became differentiated into ova.

Zavadovsky (1922), Bénoit (1924), Domm (1924), and Finlay (1925) have each shown that following the removal of the left gonad of young female chicks there is developed in the right gonadic site a testis and the bird assumes the characterization of the male. Caridroit (1925) has shown that if the ovary of the fowl is displaced or if ovarian tissue is implanted, ovarian tissue is replaced by testicular.

In addition to these experimental studies in sex-reversal, the following cases have been observed. In the case of one of the frogs resulting from the "egg-overripeness" experiments, Witschi (1923) was able to show that indeed it was a transformed female, for when mated with a normal female it sired only female offspring. This is as would be expected, if in its fundamental chromosome constitution it still remained XX, for then all its spermatozoa would be X-chromosome-bearing and on fertilizing X-bearing eggs would yield none but XX zygotes. Crew (1921) had previously encountered a similar case in the frog. It was a male used for breeding and when post-mortemed was found to be a "hermaphrodite" with degenerate ovaries and functional testes. Among its offspring were none but female. Witschi (1921) was able to show that in the case of another hermaphroditic frog both functional ova and sperm, all X-chromosome-bearing, were produced.

Riddle during the years 1914–1918 had observed the first case of complete sex-reversal in the adult bird, but he did not publish an account of this case until 1924. A ring-dove (*Streptopelia risoria*) laid eleven eggs at times exactly observed between 27th January and 15th April, 1914.

During the six months following she and a male mated three times, began sitting on a nest without producing eggs, and raised young of other parents. During the following nineteen months her sex-behavior and mode of growing changed to that of a male, frequently forcing her male mate to act as a female in copulation. At twenty-two and a half months after producing her last egg, this bird and mate were transferred to a pen with a few other spent inactive doves. The male of this pair died three and a half months later, and weights and dimensions of testes were obtained. Twenty-one months after transfer, the bird died, showing very advanced abdominal tuberculosis. Two testes were found, removed, and weighed. If any residue of the original ovary remained it was wholly included in a tuberculous mass, involving spleen and liver. At the time of autopsy this bird was supposed to be the original male of the pair, and therefore the testes were not saved for demonstration. The bird had lived forty-four and a half months after producing the last egg, became tuberculous, assumed male behavior, the curve for the body weight during the three years undergoing a remarkable change, and at death it possessed two unmistakable testes. Riddle interprets this transformation as the result of the increased metabolism which followed the destruction of the ovarian tissue and the presence of tuberculosis.

Crew (1923) described the case of a Buff Orpington hen, the reputed mother of many chickens, which when three years old was attacked by tuberculosis and developed male characters, to become a fecund male and the father of two chickens. Post-mortem examination revealed the presence of two functional testes and a highly degenerate mass of ovarian tissue destroyed by tubercular disease. This case alone could not be regarded as providing conclusive proof of sex-reversal in the fowl, for during the earlier part of its life this bird had been in the possession of a private breeder concerning whose integrity there is no doubt but whose powers of critical observation can, of course, be held up to question. However, Crew (1923) and Fell (1923) examined a series of sexually abnormal fowls and were able to demonstrate that the condition found in these could logically be interpreted as stages in the process of transformation from a female type of sex-organization to a complete male type. Similar cases have been described by Bronté Gatenby (1924) and Parkes and Brambell (1926).

More recently, the writer has examined three fowls which have been in his possession for two years or more. These were sent to him by private breeders as "hens which had become cocks." One of them was a carefully trapnested and legbanded White Leghorn hen which, it was stated, had laid 111 eggs in her second year. Each of these birds when received was imperfectly male as far as the plumage characterization was concerned, far more like a hen than a cock in shape, stance and length of long bones. Each rapidly assumed the complete male plumage and sexual behavior. They were tested for fertility and proved to be fecund when mated with normal hens. Efforts were made to raise a great number of chickens from these pens in order to examine the sex-ratio of the offspring, but, since the numbers were small and infertility common, it was not found to be practicable to raise a sufficient number. By the application of the Manoilov test to these birds an intermediate reaction was obtained which approached the female much more closely than the male. Post-mortem examination revealed a perfect male sex-equipment, no sign of ovary or of oviduct being found.

(Naturally, therefore, the accounts of the private breeders who had sent in these birds were queried, but they insist that their observations and statements are authentic.) It is possible that certain of these birds were nothing but late maturing cocks but one cannot refuse to consider the possibility that complete sex-reversal in the fowl does occur fairly commonly and that when such a bird is finally examined no morphological evidence of persisting ovary and oviduct will be found. An appeal to cytological differences between male and female does not help, and as yet the biochemical identification of sex is not sufficiently delicate.

In the mammal complete sex-reversal cannot occur in post-embryonic life, because of the differential mode of development of the internal and external genitalia. If urogenital cleft and genital tubercle become scrotum and penis, these cannot become dedifferentiated and develop anew into vulva and clitoris. If the Wolffian duct derivatives proceed to full differentiation and those of the Müllerian ducts undergo atrophy there cannot later be a reversal of these processes.

A consideration of these instances of sex-reversal will show that in the egg stage and in the post-embryonic stage of Amphibia and in the case of fish also, if Huxley's interpretation of Boulenger's results is correct, reversal can occur in either direction, female to male, and *vice versa*, whereas in the post-embryonic stage of birds it has thus far been demonstrated in one direction only, from the digametic sex to the monogametic. In this connection it is of interest to note that in the instances of intersexuality in *Lebistes* observed by Winge (1927) the change occurred in old females which assumed male characters though still breeding as normal females. That this is so is provocative of thought. It is possible that the balance between male and female sex-differentiating reactions is more easily disturbed in the case of the sex which possesses but a single X-chromosome, a suggestion which is in line with the observation of Haldane (1921) that in the case of specific and wide varietal crosses if among the offspring one sex is absent, rare, or sterile, that sex is the digametic.

In the case of Amphibia, fishes, and birds, the conditions required for complete sex-reversal are readily met. In the Amphibians and birds it has been shown that it is possible experimentally to masculinize a female and to feminize a male by appropriate gonad implantation. Male and female accessory sexual apparatuses and external genitalia are very similar, the sexual differences commonly being nothing more than differences in the degree of development of common structures, or, in the case of such as are developed from different rudiments, the set appropriate to the alternative sex becoming completely atrophied. All that is required is that one kind of gonadic tissue shall be replaced by the alternative kind. In the case of the Amphibia if, as seems the case, at the end of the breeding season the gonads are physiologically exhausted, if the differentiated tissues undergo complete involution so that a new proliferation of germinal epithelium is required for the provision of gametes for the following breeding season, or if only a portion of the primordial germ cells develop each year, then the mode of differentiation of each season's crop can be determined by the impress of varying environmental circumstances, if these are of such a nature as to disturb sufficiently the general metabolism of the individual. Such would appear to be the explanation of Champy's results. Surgical removal of the gonad (*i.e.*, removal of the differentiated germinal epi-

thelium) will lead to the same result if following gonadectomy the general metabolism of the individual is influenced by special feeding (Harms, 1923).

appearances suggest that so long as growing oocytes are present these invading sex-cords do not develop further into functional germinal tissue, perhaps being

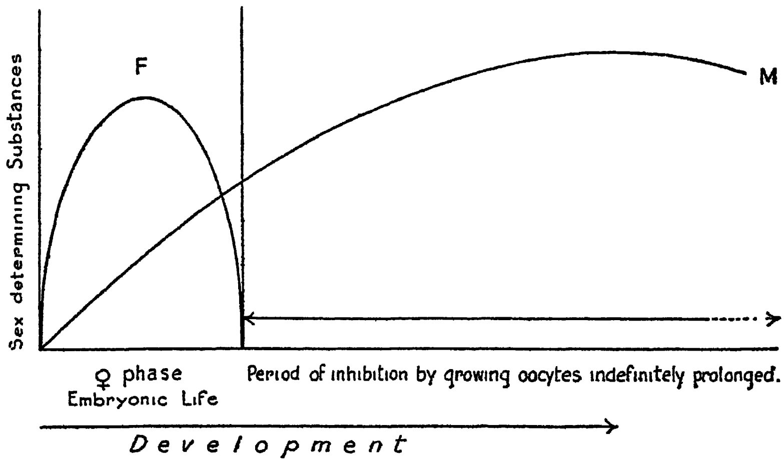

Fig. 1.

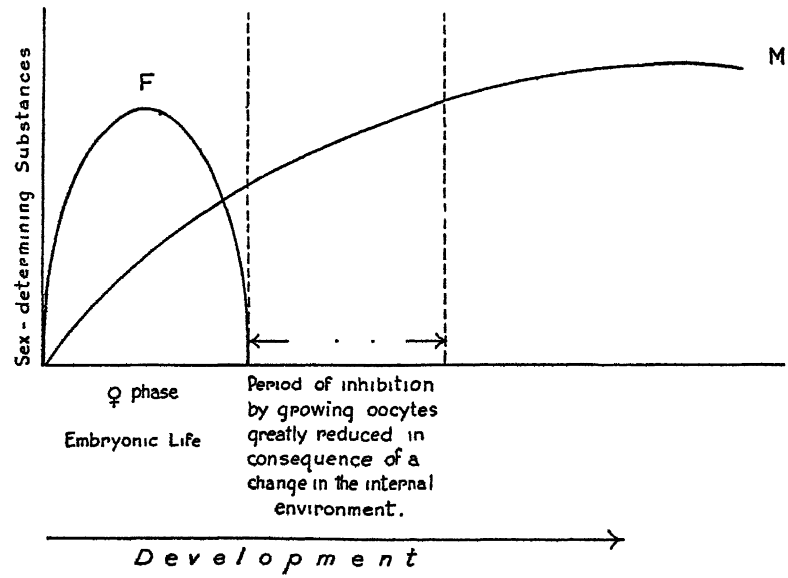

Fig. 2.

In the case of the fowl it has been shown that there are successive invasions of the organ by sex-cords derived from the peritoneum (Fell, 1923). The histological transformed into "luteal" cells. But in the absence of growing oocytes these cords are apparently converted regularly into seminiferous tubules. It would seem

that the physiological conditions which in the female embryo at the time of differentiation of the sex-organization induce the primitive germ-cells to assume the characters of oocytes—and it will be remembered that in the fowl these are laid down before birth—no longer obtain in the mature bird, so that if what may legitimately be regarded as some inhibiting influence of the functional ovary upon the invading sex-cords be removed, as is the case in ovarian atrophy and disease, or, to put the matter differently, if by certain ovarian diseases the conditions favorable for the continued development of the sex-cords are created, the germ-cells inevitably take on the characteristics of spermatogonia, spermatocytes, and spermatozoa.

If during embryonic life the female-determining substances are effectively in excess and the differentiation of the gonad and the rest of the sex-equipment proceeds under the influence of the female-differentiating reactions the oocytes are laid down. Ordinarily during the succeeding years of the individual's life the growth of the oocytes precludes the operation of the male-differentiating reactions which are increasing in efficiency. But should the conditions be unfavorable for their growth, or should conditions favorable for the continued development of the sex-cords arise as a result of the physiological exhaustion consequent upon excessive egg laying or from haemorrhage or tumor growth, then, in the absence of the inhibitory influence of the growing oocytes, the male-differentiating reactions become effective, spermatic tissue is differentiated, and the characters of the individual become as those of the male. It can be expected that almost any hen of a highly fecund strain will sooner or later develop some degree of the male characterization.

The fact that following ovariotomy of the hen there is developed in the right gonadic site a testis, is to be explained on the assumptions that (1) ovariotomy is followed by a significant modification of the basal metabolism of the individual; (2) the metabolic level which becomes established is that at which differentiation of gonadic tissue can proceed; (3) ovarian tissue is developed solely from a proliferation of germinal epithelium which follows upon a degeneration of the products of a previous proliferation that occurs about the sixth day of incubation, that the difference between differentiation into ovarian or into testicular tissues is a reflection of a difference inherent not in the tissues themselves but in the internal environment in which the original ambivalent tissue develops, and that at no other time save at about the sixth day of incubation are those conditions provocative of ovarian differentiation ever present. All proliferations of germinal epithelium in the female fowl, save the second, lead to the production of testicular tissue. Sex-reversal is thus possible in the direction female to male.

If in a group there is a sex-chromosome sex-determining mechanism (*e.g.*, XY: XX) and if this mechanism can be overridden, then in that group it can be expected that there will be individuals genotypically of one sex, phenotypically of the other, and that these when mated to individuals in which sexual genotype and phenotype are in agreement will produce offspring among which there will be a preponderance of the sex to which the transformed parents genotypically belonged (*i.e.*, a transformed female functioning as a male will yield a preponderance of females; a transformed male functioning as a female will yield a preponderance of males). If this process of transformation affects the individuals of several generations and thereafter ceases

to act, there will be a decreasing preponderance of one sex followed by a preponderance of the opposite sex in the first generation after the close of the period during which sex-transformation has occurred and finally a sex-ratio of equality.

It is to be emphasized that, although the processes of sex-differentiation are reversible, the genotypic sex of an individual is not thereby affected. The monogametic individual remains monogametic and the digametic remains digametic, even though it elaborates sperm instead of ova. The form and function of the gamete are not determined by its chromosome content, they are determined by the structure and function of the gonad in which the gamete is elaborated.

The profound modification of sexuality induced by alterations in metabolic level has persuaded some investigators to the conclusion that sex fundamentally is not an affair of the chromosomes and genes, but that it is the physiological properties of the zygotes that determine sex; but surely it is reasonable to hold that the conditions within the cell are nothing more than the sum total of the physiological expression of the genes in action. It is in the action of the genes that this or that type of initial metabolism becomes established.

In the case of those forms in which sex-reversal is usual it would seem that the physiological state established by the genotype is readily overridden through the impress of environmental agencies and that sex-reversal is common because this is so. Reversal is an adaptive response to a changing environment—the individual is a female when it may be and a male when it must.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will usually appear in each number one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

EVOLUTION

MODERNISM. *What It Is. What It Does. Whence It Came. Its Relation to Evolution.*
By J. M. Stanfield.
The Christian Alliance Publishing Co.
\$1.50 $4\frac{3}{4} \times 7\frac{1}{2}$; 217 *New York*

So far in our *Fundamentalist Portrait Gallery* we have only had depictions of persons who, in a sense, might be called derivative Fundamentalists. This time we are pleased to be able to present in Mr. J. M. Stanfield a representative of the real, basic, autochthonous stock, a *Tennessee* Fundamentalist.

In an introduction by Professor Leander S. Keyser of the Hamma Divinity School, it is stated that Mr. Stanfield "is a layman, not a professional theologian." This seems entirely credible, after reading the book. But Professor Keyser follows it with another statement that: "He cannot, therefore, be accused of having 'an axe to grind' or a special religious bias." Here, again after reading the book, we feel compelled to part company intellectually with Professor Keyser. To us Mr. Stanfield seems, throughout his treatise, to glory in his religious bias, and to whet his axe for the necks of modernists and evolutionists with a single-minded fervor which compels our admiration for its hundred-per-cent thoroughness. He gives no quarter and asks none. There is no slopping or staining of the pages with the milk of human kindness. Mr. Stanfield knows precisely what he thinks of modernists and evolutionists and he tells them and the world.

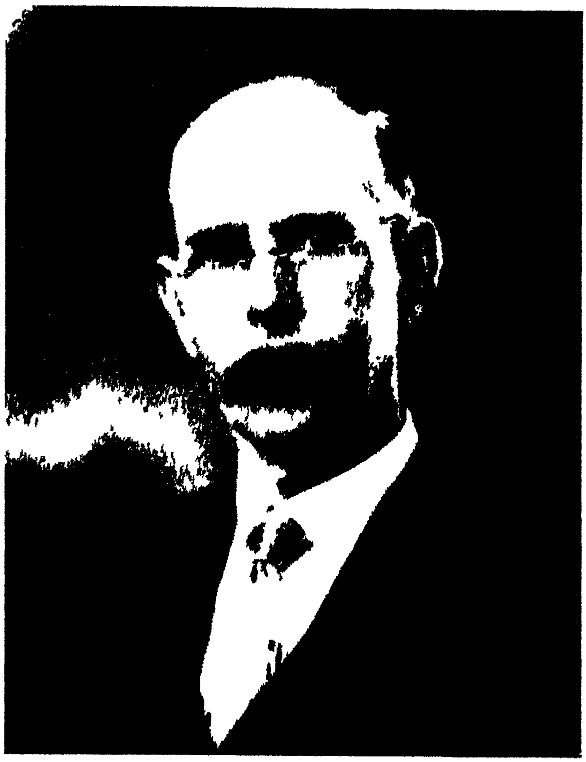
The book is divided into three parts. The first devotes itself to modernism as a theological doctrine, the second to evolution, and the third to the development of these heresies in the Protestant churches. The forthrightness of the theological position is sufficiently illustrated by the following quotation.

> Since God is all-wise and cannot lie, and is the Author of the whole Bible, according to the orthodox view; all statements in the Bible involving science or history must be true, notwithstanding the fact that the Bible was meant to teach religion. If the Bible was full of errors, as the Modernists claim, it could not reveal a God of truth nor teach righteousness. Error cannot reveal truth nor the God of truth.

Regarding evolution Mr. Stanfield has no patience with the "reconcilers." He prints a long quotation from a book by one Dr. Marion Shutter, which seems to us to be a singularly pious statement of evolution from the standpoint of a "rec-

onciler," and then proceeds to discuss it as follows:

This is Theistic Evolution. Notice some of the blasphemous heresies just this quotation includes, treats the Genesis account of the creation of man as untrue and affirms a brute origin for man; denies that man was first holy, but teaches that he emerged from the animal, a savage and without revelation from God, learned righteousness through his own efforts means that he came from the brute, but because he had the good blood of Abraham, David and the prophets in him, he becomes a good example for us! And lastly, God, men and nature are all one in essence. Shutter rather obscures this thought but you can see that it is there. So the difference between Atheistic, or infidel, evolution and Theistic evolution is just about "six of one and a half dozen of the other," both have the same origin, general principles and object



J. M. Stanfield, of Cleveland, Tennessee

and experiences. At first he was without moral responsibility, knew no God, but after "uncalendared ages" achieved the idea of one.

You notice the Bible as a revelation is ignored, and this Theistic evolutionist calls the Genesis account a "baseless fabric of a vision"! Then he shows his belief that the Bible is untrue by teaching that there has never been a curse, nor sin and fall; men are not under condemnation, no devil, no wrath of God, no hell, no need for the atonement of Christ as a substitute for sinners. Christ was not God incarnate born of a virgin, but he blasphemously teaches that Christ also is a child of evolution, which

Farther on Mr. Stanfield says:

Evolution is the result of a desire to oppose and contradict the truths of divine revelation. This is plainly and frankly stated by Huxley in *Science and Hebrew Tradition*, as follows: "These essays are for the most part intended to contribute to the process of destroying the infallibility of Scripture." And yet with all this effort of these learned skeptics, not a single known or genuinely proven fact in any department of science, history or archaeology has been found to be in conflict with the real teaching of the Bible and the Christian religion. Lord Kelvin, the

great English scientist, states it thus: "There is not a single ascertained fact of science which conflicts with any statement of the Bible." The real scientists are not skeptics. We mention a few as Kepler, Newton, Davy, Linnie Lavoisier, Maedler (who said, "A real scientist cannot be an infidel"), Virchow and our own Howard A. Kelley.

Why "Linnie Lavoisier" we cannot guess, unless it be a misprint for "Linné, Lavoisier." But it is cheering to see our friend Dr. Kelley in such high-toned company.

From this book, on which we can waste no more space, biologists will get a clearer picture of the devastating implications of the Tennessee brand of Fundamentalism than from any other we have seen. If the ideas it embodies were to prevail the Dark Ages would seem, by comparison, to have been a veritable paradise of light and learning.

THE DENTITION OF DRYOPITHECUS AND THE ORIGIN OF MAN.
By William K. Gregory and Milo Hellman.
American Museum of Natural History
$1.50 *New York*
$6\frac{1}{2} \times 9\frac{1}{2}$; 123 + 25 plates (paper)

The chief results of this beautifully illustrated, extremely thorough morphological contribution to our knowledge of the human family tree are:

To judge from the characters of the dentition the modern anthropoids, taken as a whole, are unquestionably man's nearest relatives among all known mammals; conversely, no other known living or fossil mammals can seriously contest this claim of the anthropoid group. We therefore prefer to accept this direct evidence and to trace the evolution of the human dentition through that of the primitive anthropoid *Dryopithecus* back to the primitive tarsioid *Parapithecus*, rather than to invent entirely hypothetical and unknown stages leading back to unknown stem forms of pre-primates in the Paleocene or Upper Cretaceous. Each existing anthropoid has specialized away from the common ancestor in certain izations has been made, the chimpanzee is far less specialized away from the common stem form than is man. The various extinct anthropoids known as *Dryopithecus* are decidedly nearer to the common stem form than are any of the modern giant anthropoids.

From some form of *Dryopithecus* possibly related to *D. rhenanus* man has inherited his dental formula, the "Bicuspid" pattern of the upper and lower premolars, the "*Dryopithecus* pattern" of the molars, many details of the incisors and canines and many important characters of the deciduous dentition. It may be noted that this is not a light speculation but is based on observations of the characters actually inherited in the more primitive human dentitions, apparently from a *Dryopithecus*-like ancestor.

PURPOSIVE EVOLUTION. *The Link Between Science and Religion.*
By Edmund Noble. *Henry Holt and Co.*
$5.00 (Student's edition $4.00) *New York*
$5\frac{1}{4} \times 8\frac{1}{2}$; xi + 578

A discussion of the hoary problem of teleology, by a person who can at least write well, whatever one may think of his philosophical powers. The thesis developed is that

purposiveness is a principle rooted in things, not a value at some point in time and place added to things—as the ways in which, through directed motion, ends are reached in both animate and inanimate, not as the consciousness of such ways. The vital activities of the organism, internal and relational, unconscious and conscious, are seen to derive from the self-maintaining activities of the universe; their purposive character is traced to a cosmos which is end-reaching before the coming of life and "intelligent" before the advent of consciousness. Natural selection, while retained as an eliminating factor, is relieved from the impossible task of giving rise to those variations which it only helps to conserve but cannot have any part in originating: by advance beyond the Darwinian theory to recognition of a purposive process in Nature we are enabled to pass from the "origin of species" to the origin of the organism, and from an obviously inevitable "survival of the fittest" to realization of why and how the fittest arrive.

This argument can, of course, arrive only at one terminus—God. It fails entirely to answer the impudent question

first raised by a paleolithic school boy in the Academy at Les Eyzies: "If God is responsible for the purposiveness observable in the order of nature, who, then, made God?"

THE NATURE OF THE WORLD AND OF MAN.

By Sixteen Members of the University of Chicago Faculty.
H. H. Newman, Editor.

The University of Chicago Press
$4.00 6 x 8¾, xxiv + 566 *Chicago*

The specifically biological chapters in this latest addition to the now so popular type of coöperative literature are the following: The Nature and Origin of Life, and The Factors of Organic Evolution, by H. H. Newman; The Bacteria, by E. O. Jordan; The Evolution of the Plant Kingdom, by M. C. Coulter; Interactions between Plants and Their Environment, by H. C. Cowles; The Evolution of the Invertebrates, by W. C. Allee; The Evolution of the Vertebrates, by Alfred S. Romer; The Coming of Man, by F.-C. Cole; Human Inheritance, by E. R. Downing; Man from the Point of View of His Development and Structure, by G. W. Bartelmez; The Dynamics of Living Processes, by A. J. Carlson; Mind in Evolution, by C. H. Judd. The book is the outcome of a general "survey" course. The quality of the different contributions naturally varies. But taken as a whole the book has real, if ephemeral, value.

SPIRITUAL EVOLUTION AND THE BIBLE.

By Edna F. Lee.

The Christopher Publishing House
$1.00 5 x 7½; 44 *Boston*

It is probable that the late Mr. Bryan would have held this sincere little tract in as low esteem as he did the writings of scientific men. It is a reconciliation document by a deeply religious person. Reconciliation is here achieved in the simplest of conceivable ways. All the results of science, past, present and future, whatever they may be, are cheerfully and naively accepted at their face value. They are held to represent the awkward and groping approach of mankind to a realization and understanding of what God's plan was and is. "We need not know the details of the theory of Evolution to believe in the general principle, for the world before us is saturated with proof of the struggle upward, and not only physically but spiritually." Mrs. Lee is obviously neither a great scholar nor a great philosopher. She probably does not in the smallest degree realize how similar her cosmic philosophy, arrived at by the simplest minded faith, is to that of some of the profoundest thinkers who have struggled with the problem. Her terminology is, to be sure, different from theirs. But that is unimportant.

GENETICS

ELEMENTE DER EXAKTEN ERBLICHKEITSLEHRE. *Mit Grundzügen der Biologischen Variations-statistik.*

By W. Johannsen. *Gustav Fischer*
Mk. 32 *Jena*
6½ x 9½; xi + 735 (paper)

The third edition of this classic of genetics appears thirteen years after the second, which has been out of print for more than seven. Naturally much revision has been required. Genetics has made great strides in the last decades. But the general plan of the "thirty lectures" remains much as before, which

means that the book is broader in the distribution of its emphasis than are some of the current American and English texts on genetics. Johannsen made a very great contribution to our knowledge of heredity. The interest of biologists in this field has swung in another direction and his work has in some sense been overshadowed. But its fundamental soundness and importance has not in the least been altered by this circumstance.

POTATO VARIETIES.
By Redcliffe N. Salaman.

The Macmillan Co.
$8.50 7 x 10¼; xxii + 378 *New York*

A thorough, sound, and penetrating contribution to plant genetics, by the foremost investigator of the field covered. For twenty years past Dr. Salaman has devoted himself to the study of the genetics of the potato. In this book he summarizes and critically evaluates, from the background of this rich experience, a great deal of what is known of the subject. The first twenty-three chapters deal with the general genetic problems which arise in connection with the cultivation of this important crop, while the remainder of the book deals with the description, history and synonomy of European varieties. There is a bibliography of 177 titles, and a detailed index. The book is illustrated with nine plates, beside text figures.

BREEDING AND IMPROVEMENT OF FARM ANIMALS.
By Victor A. Rice.

McGraw-Hill Book Co., Inc.
$3.50 5¾ x 9; xiv + 362 *New York*

A text book of animal breeding for use in agricultural colleges. It follows conventional lines in the treatment of the various topics covered, but good pedagogical judgment is shown in the arrangement of the material. Emphasis is rightly placed, considering the purpose of the book, on the practical aspects of the subject.

ÜBER DIE ZEICHNUNGEN DER BLÄTTER UND BLÜTEN.
By Ernst Küster.

Urban und Schwarzenberg
Rm. 7.20 *Berlin*
7 x 10; iv + 82 (paper)

A systematic discussion of variegation in leaves and blossoms, with numerous photographic illustrations. It will prove a useful reference work for plant geneticists. There is an index of genera only.

GENERAL BIOLOGY

LOCAL IMMUNIZATION. *Specific Dressings.*
By A. Besredka. Edited and translated by Harry Plotz. *The Williams & Wilkins Co.*
$3.50 5½ x 8¾; xi + 181 *Baltimore*

This is an important book, containing a great deal of original and interesting material, but it is written with so little sense of literary form that it leaves an impression of general vagueness and lack of precise thinking. This is most unfortunate because the author's experimental work and the theoretical conclusions to which it has led, are in the highest degree important. They amount really to a complete alteration of currently accepted views regarding the biology of immunity. Besredka believes that immunization is essentially a local phenomenon. Thus in the case of such diseases as dysentery,

typhoid fever, paratyphoid or cholera, he pictures the phenomenon in this way:

> There exist in the various organs of higher animals, highly differentiated cells which act as local phagocytes. These cells enter into reaction only with certain definite viruses, contrary to the action of the leucocytes or motile phagocytes. The latter attack indiscriminately all foreign bodies; whether they be living or dead.
>
> It is these receptive cells, which are the exclusive property of highly differentiated beings, that have a specific affinity for certain viruses. It is fixed phagocytes—cells of the reticulo-endothelial layer, intestinal lymphatic cells or other cells—that direct the chemotactic movement of the free phagocytes and assure, with the aid of the latter, the immunity of the entire animal organism.

The book will well repay reading.

SYMBIONTICISM AND THE ORIGIN OF SPECIES.
By Ivan E. Wallin.
The Williams & Wilkins Co.
$3.00 $6\frac{1}{4} \times 9\frac{1}{4}$; xl + 171 *Baltimore*

"Symbionticism" is a term coined by Wallin to indicate the "universal presence of microörganisms within the cells of all plants and animals." It is the end result of "prototaxis," which is defined as "the innate tendency of one organism or cell to react in a definite manner to another organism or cell." This theory of symbionticism is based on the assumption that mitochondria are bacterial in nature. The author set out in 1919 to prove this and evidently convinced himself that mitochondria are really bacteria. On this assumption he proceeds to explain practically all of the fundamental problems of biology, including the phenomena of heredity and organic evolution. So far as known to the reviewer no first-rate investigator agrees with him. The book contains a considerable amount of interesting material on mitochondria and symbiosis.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 213.* Containing following articles: *Histologische Methoden und Ergebnisse der Mikroskopie im auffallenden Licht*, by Paul Vonwiller; *Die Nuclealfärbung*, by Robert Feulgen; *Verfahren, um den isolierten Hundekopf durch Anastomose mit dem Blutkreislauf eines anderen Hundes überlebend zu halten*, and *Perfusion des "isolierten" Kopfes vom "isolierten" Herz-Lungen-Präparat aus beim selben Hund*, and *Verfahren zur Hyper- und Hypothermisation der Säugetiere durch Erwärmung und Abkühlung des Blutes des durch Anastomose verbundenen carotidojugulären Kreislaufes*, and *Versuchsanordnung zur fraktionierten und kontinuierlichen quantitativen Bestimmung des CO_2 der Exspirationsluft*, by J. F. Heymans and C. Heymans; *Die Verwendung isolierter, lebender Membranen zum Studium der Permeabilität*, by Ernst Wertheimer; *Das Prinzip des absoluten Optimums in der vergleichenden Physiologie*, by Väinö Krohn.
Urban und Schwarzenberg
Mk. 7.80 7 x 10; 156 (paper) *Berlin*

This number of the Abderhalden handbook deals with a wide range of subjects, not closely related to each other. The last essay in the volume is an important one, which should be read by every experimentalist. It is a first rate contribution to scientific methodology.

ESSAYS IN POPULAR SCIENCE.
By Julian Huxley. *Alfred A. Knopf, Inc.*
$4.00 *New York*
$5\frac{1}{2} \times 8\frac{1}{2}$; xvi + 316

These essays, which cover a wide range of subjects, make pleasant and easy reading, and would seem likely to captivate such an audience as that of the Atlantic Monthly, for example. The professional biologist will be here and there shocked

at the easy and graceful sureness about matters which he had supposed were not only debatable but actively under debate. This attitude seems to be regarded as essential to successful popular scientific writing, and we accept it as we do many other current manifestations of the *mores*, which we cannot quite rationalize. But it *is* difficult to be properly serious when we are told that why more boy babies die is because boys have more semi-lethal genes in their chromosomes than do girls!

A BIBLIOGRAPHY OF AMERICAN NATURAL HISTORY. *The Pioneer Century, 1769–1865. The Rôle Played by the Scientific Societies; Scientific Journals; Natural History Museums and Botanic Gardens; State Geological and Natural History Surveys; Federal Exploring Expeditions in the Rise and Progress of American Botany, Geology, Mineralogy, Paleontology and Zoology.*

Vol. I. An Annotated Bibliography of the Publications Relating to the History, Biography and Bibliography of American Natural History and its Institutions, during Colonial Times and the Pioneer Century, which have been published up to 1924; with a Classified Subject and Geographic Index; and a Bibliography of Biographies.

Vol. II. The Institutions which have contributed to the Rise and Progress of American Natural History, which were Founded or Organized between 1769 and 1844.

By Max Meisel.

The Premier Publishing Co.
Brooklyn, N. Y.

Vol. I, \$5.00 $5\frac{3}{4} \times 9$; 244
Vol. II, \$7.50 $5\frac{3}{4} \times 9$; xii + 741

This is a monumental piece of exact and painstaking bibliographical research, which will be an invaluable resource to the student of the history of science in America. A third volume is yet to appear. In the second volume the detailed citation of papers relating to natural history is preceded by a brief but extraordinarily useful history of the society or institution which published them. American biologists cannot do less to express their appreciation of the colossal labors of Mr. Meisel in their behalf than to see to it that a complete set of this Bibliography is on the shelves of their libraries.

THE MEMORY FACTOR IN BIOLOGY. *A Sketch of the Unity of Life.*
By C. J. Patten. Baillière, Tindall and Cox
5 shillings $4 \times 6\frac{1}{2}$; xiii + 175 *London*

This book, like its author's "Passing of the Phantoms," reviewed in these pages last year, contains a lot of matter about the habits and behavior of animals, particularly birds, which is interesting, if not always very critical. The general thesis of the book is to support the views of Hering, Samuel Butler, Semon, and Rignano, regarding the biological importance of memory.

LE BACTÉRIOPHAGE ET SON COMPORTEMENT. *Deuxième Édition.*
By F. d'Hérelle. Masson et Cie.
\$1.72 $6\frac{1}{2} \times 10$; 551 (paper) *Paris*

A revised second edition of d'Hérelle's well-known treatise. A notice of the English translation has already appeared in THE QUARTERLY REVIEW OF BIOLOGY. It is a book which no student of general biology should fail to read, whether he is otherwise interested in immunology or not.

DER NEO-DARWINISMUS *metaphysisch begründet durch das Allgemeine Zweckmässigkeitsgesetz.*
By Victor Schiffner. Gustav Fischer
Mk.2 $6\frac{1}{4} \times 9\frac{1}{4}$; 50 (paper) *Jena*

A philosophical discussion of adaptation. The author's "Neo-Darwinism" has a somewhat different connotation than that implied in the usual use of the word. He proposes to use this term to cover all "laws" which have to do with changes of living things, and under its aegis to synthesize all these into one "*Allgemeine Zweckmässigkeits-Gesetz*."

THE MEANING OF DISEASE. *An Inquiry in the Field of Medical Philosophy.*
By William A. White.
The Williams & Wilkins Co.
\$3.00 $5 \times 7\frac{1}{2}$; 220 *Baltimore*

An interesting, well-written philosophical speculation regarding the biology of health and disease. Biologists will probably furnish a more sympathetic audience for the book than will most physicians, who as a group are, at the moment, thinking in different channels than Dr. White.

FATALISM OR FREEDOM. *A Biologist's Answer.*
By C. Judson Herrick.
W. W. Norton and Co., Inc.
\$1.00 $4\frac{3}{4} \times 6\frac{1}{2}$; 96 *New York*

The conclusion reached is that "A denial of the reality and efficacy of my power to shape my own character in accordance with consciously fabricated ideals and so to exercise genuine freedom to enlarge, purify, and ennoble my personality is a reversion to a primitive and tawdry fatalistic mythology of a barbarous age."

Sub specie aeternitatis Benedictus de Spinoza damnatus est.

BRIEF BIOLOGY.
By Charles Gramet (revised in collaboration with John F. Hummer). *Globe Book Co.*
67 cents *New York*
$5 \times 7\frac{1}{4}$; v + 218 (paper)

This text book of biology is "brief" in the sense that the economy of diction appropriate to telegraphic communication is used to convey to students of high-school grade a working knowledge of the plant and animal kingdoms in their entirety, including anatomy, physiology, psychology, anthropology, medicine, public health, etc. Perhaps this is sound pedagogy, but it wears a ghastly mien.

DE LA DURÉE DES ÊTRES VIVANTS. *Facteurs qui relèvent ou abaissent l'énergie vitale, qui prolongent ou raccourcissent la vie.*
By Éd. Retterer. *Gaston Doin et Cie.*
10 francs $5\frac{1}{2} \times 9$; 188 (paper) *Paris*

A review of the literature on the biology of senescence and death, with particular emphasis on the rôle of the endocrine organs in these matters, and with a more sympathetic attitude towards the potentialities of surgical procedures as a means of rejuvenation than many biologists are disposed at present to assume.

GENERAL AND PROFESSIONAL BIOLOGY *with Special Reference to Man. Vol. I, General Biology. Vol. II. Introductory Embryology (Chick, Frog, and Mammal) and Comparative Anatomy.*
By Edward J. Menge.
The Bruce Publishing Co.
Vol. I, \$3.50 6×9; 484 *Milwaukee*
Vol. II, \$4.00 6×9; 498

The second edition of a text book of biology which, in a number of particulars, follows novel lines. The range

covered is enormous, the treatment of each subject is telegraphic in its brevity, and the rhythm of the composition is syncopated. It is a curious book.

HÄMATOLOGISCHES PRAKTIKUM. *Für Studierende und Ärzte.*
By Hans Ziemann. *S. Karger*
M. 7.20 $5\frac{1}{2}$ x $8\frac{1}{2}$; viii + 166 *Berlin*

A comprehensive, though brief, practical handbook on the general biology and pathology of the blood, with technical directions for the study of these subjects.

HUMAN BIOLOGY

RITUAL AND BELIEF IN MOROCCO. *Volumes I and II.*
By Edward Westermarck.
The Macmillan Co.
$15 for set *New York*
$5\frac{1}{2}$ x $8\frac{1}{2}$; Vol. I, xxxii + 608
Vol. II, xvii + 629

The author of *The History of Human Marriage* makes a contribution in the present volumes destined to rank as of perhaps even greater significance than his former work, which has long been a reference classic in the field of human biology. Professor Westermarck went to Morocco in 1898, as the first stop on a contemplated journey to various countries "to acquire first-hand knowledge of some forms of culture which differ from our own." He never went any farther. In the period between 1898 and 1926 he has made 21 journeys to Morocco, and spent there altogether seven years. The knowledge gained in this long, repeated, and intimate association with the Moroccans is embodied in this book. It is a contribution of the very first rank to anthropology, ethnology, psychology, and sociology. In addition to the author's wide and penetrating observations at first-hand, he has an encyclopedic knowledge of the literature, and every point is correlated and integrated with prior knowledge, with precise documentation. There is a really satisfactory index, covering 69 pages close set in eight point type. Altogether this is a monumental work, as interesting as it is sound. Our more wicked readers will find Chapter IX, "Curses and Oaths," not only entertaining but perhaps, on occasion, useful. We have something to learn from the Moroccans in this branch of polite accomplishments.

THE HISTORY OF WITCHCRAFT AND DEMONOLOGY.
By Montague Summers.
Alfred A. Knopf, Inc.
$5.00 6 x 9; xv + 353 *New York*

How this curious treatise came to get incorporated into the *History of Civilization* series is difficult to understand. For it is a theological tract in defense of witchcraft, *by one who believes in witches!* In making this statement our only defense against the charge of spoofing is the book itself. Read it!

And this is not all:

> Modern Spiritism is merely Witchcraft revived. The Second Plenary Council of Baltimore (1866), whilst making ample allowance for prestidigitation and trickery of every kind, warns the faithful against lending any support whatsoever to Spiritism and forbids them to attend seances even out of idle curiosity, for some, at least, of the manifestations must necessarily be ascribed to Satanic intervention since in no other manner can they be understood or explained.

The book is enormously erudite. The annotation and documentation is colossal, the bibliography extending to over 30 pages of fine print. The answer to the

old query "Can you beat it?" is clear. You can't!

GENIUS. *Some Revaluations.*
By Arthur C. Jacobson. *Greenberg*
$2.50 $5\frac{1}{4} \times 8\frac{1}{4}$; 160 *New York*

This is an entertaining book, which will be instantly condemned to the Index as blasphemous and heretical by every orthodox eugenical pontiff. For its thesis is that: "It is in the outcast, disinherited, vagabond, criminal, defective, insane and generally abnormal elements of humankind that genius germinates, never in the well-bred, eugenically speaking, Right Wing of the race. Let the 'respectable' wince if galled by this challenging truth."

The word "never" seems to us unfortunate in the first sentence quoted. But an author who has assembled such an interesting lot of evidence as Dr. Jacobson has, may perhaps be permitted a little exuberance. It is unfortunate that his book will not be much read by eugenists.

NATIVE DIET. *With Numerous Practical Recipes.*
By Ettie A. Rout. *William Heinemann*
6 shillings $5\frac{1}{4} \times 8\frac{1}{2}$; ix + 140 *London*

Like everything that Ettie Rout writes this book is interesting. It is propaganda for modified vegetarianism. The only meat food recommended is the flesh of fish or birds. About half the book is devoted to a discussion of the food habits of the Maori before contact with civilization, and the other half with recipes. The book ought not to be allowed to circulate in the United States because it contains the following sentences, which can only be regarded as an insult to the Constitution: "Our personal health would greatly improve if we took light herbal beers (home-made) instead of the large quantities of strong tea and coffee many of us drink. Home-brewed ale is a natural aperient. . . . . Ales and beers are very little trouble to make—there are plenty of recipes available—and when made at home they are extraordinarily cheap."

PRINCIPLES OF HUMAN GEOGRAPHY.
By P. Vidal de la Blache. Edited by Emmanuel de Martonne. Translated from the French by Millicent T. Bingham.
Henry Holt and Co.
$5.00 (Student's edition $4.00) $5\frac{1}{2} \times 8\frac{1}{2}$; xv + 511 *New York*

Vidal de la Blache was the founder of the modern French school of geography, which in some important respects leads the world in this field. The present work is posthumous. The manuscript was in a highly unfinished state at his death, and while the completion by other hands has been skilfully done, it is obviously not the book that it would have been if its author could have finished it. It is a distinct service to have made so excellent an English translation as this is. A good deal of the author's salty style has been preserved. Students of the population problem, and of human biology generally, will want to read it.

ORIGINS OF EDUCATION AMONG PRIMITIVE PEOPLES. *A Comparative Study in Racial Development.*
By W. D. Hambly. *The Macmillan Co.*
$7.50 $5\frac{3}{4} \times 8\frac{3}{4}$; xx + 432 *New York*

The education of primitive children proceeds along lines similar to the education of wild animals. Through play activities, with a certain amount of parental correction and guidance, the

young savage learns how to avoid at least the major dangers which lurk in the biological and physical environment, and how to turn cosmic forces and situations in some degree to his advantage. It is a useful thing to have the scattered information on the education of primitive children collected, and critically organized and evaluated as it is in this interesting and sound treatise. The book is copiously illustrated with excellent photographs, and has an extensive bibliography and index.

DAS PROBLEM DER MENSCHWERDUNG.

By L. Bolk. *Gustav Fischer*
2.10 marks $6\frac{1}{2}$ x $9\frac{1}{2}$; 44 (paper) *Jena*

In this lecture before the 1926 meeting of the German Anatomical Society, the distinguished author points out that the problem of human evolution has two sharply separated aspects. One is the phylogenetic relationship of man to the other primates. The other is the genesis of the human form. It is the second of these problems with which he is concerned. He develops the thesis that the human form is the resultant of a progressive evolutionary "fetalization," the causal factors for which are to be found in the endocrine system.

THE SIGNIFICANCE OF THE PHYSICAL CONSTITUTION IN MENTAL DISEASE.

By F. I. Wertheimer and Florence E. Hesketh.
The Williams & Wilkins Co.
$2.50 *Baltimore*
6 x 9; xiii + 76 + 5 plates

This study of the relation of physical constitution to mental disease is based upon the careful anthropometric measurement of a long series of bodily dimensions in nineteen cases of affective (manic-depressive) psychopathic personalities and psychoneuroses; and ten cases of organic reaction type including epilepsy. A new index is described, which is said to differentiate "exactly" the clear asthenic, athletic, and pyknic types of Kretschmer. There is a bibliography of 95 titles, but no index.

INFANT MORTALITY AND ITS CAUSES. *With an Appendix on the Trend of Maternal Mortality Rates in the United States.*

By Robert M. Woodbury.
The Williams & Wilkins Co.
$3.50 $5\frac{5}{8}$ x 8; x + 204 *Baltimore*

This book is mainly a reprint of separate papers on various aspects of infant mortality, originally published while the author was statistician of the Childrens' Bureau of the Department of Labor in Washington. It contains a considerable amount of material of interest to the student of human biology, though it makes no considerable addition to already existing knowledge. There is a detailed index.

AN INTRODUCTION TO THE HISTORY OF MEDICINE. *From the time of the Pharaohs to the end of the XVIIIth Century.*

By Charles G. Cumston. With an Essay on the relation of History and Philosophy to Medicine by F. G. Crookshank.
Alfred A. Knopf, Inc.
$5.00 6 x 9; xxxii + 390 *New York*

A history of medicine intended primarily for the general reader, and secondarily as an introduction to the subject for the student of medicine. Both these purposes it serves extremely well. It is

one of the happiest additions which the English editor of *The History of Civilization* series (Mr. C. K. Ogden), has made to the French series *L'Évolution de l'Humanité*.

UNFRUCHTBARKEIT ALS FOLGE UNNATÜRLICHER LEBENSWEISE. *Ein Versuch, die ungewollte Kinderlosigkeit des Menschen auf Grund von Tierversuchen und anatomischen Untersuchungen auf die Folgen des Kulturlebens zurückzuführen.*
By H. Stieve. *J. F. Bergmann*
RM. 3.60 $6\frac{3}{4}$ x 10; 52 (paper) *Munich*

Describes a series of experimental investigations showing the deleterious effects of bad environmental conditions, poisons, inadequate food, bad housing, etc. upon the gonads of rats, poultry, etc. From these results the conclusion is reached that the "unnatural" environmental conditions of modern civilization are a major factor in the decline of the human birth-rate. The evidence does not quite prove the conclusion.

VERHANDLUNGEN DER GESELLSCHAFT FÜR PHYSISCHE ANTHROPOLOGIE. *Vorträge gehalten am 13. und 14. April 1926 auf der ersten Tagung in Freiburg i. B. Band I.*
Herausgegeben vom Vorstand der Gesellschaft. Anthropologischen Institut der Universität München
Mk. 6 *München*
$6\frac{1}{2}$ x 10; 78 + 10 plates (paper)

This report of the first meeting of the German Society for Physical Anthropology contains ten interesting papers by members. It is a pleasure to call the attention of American workers to this new society and its publication. These facts testify to the growing recognition of physical anthropology as a special and separate discipline. The *Verhandlungen* are published as a supplement to Volume III of the *Anthropologischer Anzeiger*.

THIS BELIEVING WORLD. *A Simple Account of the Great Religions of Mankind.*
By Lewis Browne. *The Macmillan Co.*
\$3.50 $5\frac{1}{2}$ x $8\frac{1}{2}$; 347 *New York*

This "best seller" is an entertaining contribution to human biology. It tells the story of the manner in which the world's great religions developed, with especial emphasis on the basic motivating element, fear of Nature and its phenomena. We recommend the book strongly to the young. We have seen no better prophylaxis against Fundamentalism.

HYGIEIA *or Disease and Evolution.*
By Burton P. Thom. *E. P. Dutton and Co.*
\$1.00 $4\frac{1}{4}$ x 6; 107 *New York*

This number of the Today and Tomorrow series discusses the evolution of disease and its influence upon the past and future evolution of man. The general conclusion reached is that a "gloriously golden" future impends, "when misery will be no more, and peace, and health, and happiness will reign supreme." We hope the author is right about this.

KIND UND VOLK. *Der Biologische Wert der Treue zu den Lebensgesetzen beim Aufbau der Familie. Erster Teil, Vererbung und Auslese. Zweiter Teil, Gestaltung der Lebenslage.*
By Hermann Muckermann.
Herder und Co.
Freiburg
Teil 1, Mk. 3.60 5 x $7\frac{1}{2}$; xii + 253
Teil 2, Mk. 3.80 5 x $7\frac{1}{2}$; 290

The "11th to 15th" edition of a treatise

for the general reader which deals with eugenics in the first volume, and a queer mixture of patriotism, babies, housing conditions and religion in the second. It seems unlikely to be of particular interest to American readers, but since over 28,000 copies have been sold there must be something about it which the Germans like.

CONSIDERATIONS REGARDING THE POSSIBLE RELATIONSHIP OF CANCER TO RACE BASED ON A STUDY OF ANTHROPOLOGICAL AND MEDICAL STATISTICS OF CERTAIN EUROPEAN COUNTRIES.
By Alfredo Niceforo and Eugène Pittard.
Health Organization, League of Nations
$3.00 $8\frac{1}{4}$ x $10\frac{1}{4}$; 330 *Geneva*

A most interesting study of the incidence of cancer, by a distinguished statistician and a distinguished anthropologist, working in collaboration. They are extremely cautious about drawing general conclusions, but the evidence they present certainly makes it probable that "the Mediterranean 'race' (*Homo mediterraneus*) is less subject to cancer than the Alpine 'race' (*Homo alpinus*) or the blond dolichocephalous 'race' (*Homo nordicus or europaeus*)."

DE LAMAR LECTURES 1925–1926. *The Johns Hopkins University, School of Hygiene and Public Health.*
Edited by W. H. Howell.
The Williams and Wilkins Co.
$5.00 6 x 9; 220 *Baltimore*

The papers in this collection of lectures on problems of hygiene and public health likely to be of greatest interest to the biologist are those of Smillie on "Intensity surveys of hookworm infestation," Goldberger on the "Etiology of pellagra," Dublin on "Body build and longevity," and Stockard on "Constitutional types in relation to disease."

CALIFORNIA ANTHROPOMETRY.
By Edward Winslow Gifford.
University of California Press
$2.25 *Berkeley*
$7\frac{1}{4}$ x $10\frac{3}{4}$; 173 + 52 plates

This volume presents an extensive series of measurements of California Indians and the constants, chiefly means, calculated from them. These data have been collected at various times during the past twenty years by members of the Department of Anthropology of the University of California. The plates present a great number of photographs of Indian types.

THE ARAB CIVILIZATION.
By Joseph Hell (Translated from the German by S. Khuda Bukhsh).
W. Heffer and Sons, Ltd.
8s.6d. *Cambridge*
$5\frac{1}{2}$ x $8\frac{1}{2}$; xvii + 128

Professor Hell's *Die Kultur der Araber* is an interesting account of the history of Mohammedanism, and its social consequences. This translation is well done, and derives added interest from the fact that the translator debates a number of points with his author.

THE EVOLUTION OF VALUES. *Studies in Sociology with Special Applications to Teaching.*
By C. Bouglé. Translated by Helen S. Sellars.
Henry Holt and Co.
$2.00 *New York*
$4\frac{3}{4}$ x $7\frac{3}{8}$; xxxvii + 277

An interesting, well documented and indexed discussion of human society from

the point of view of the significance of moral and various other sorts of values upon social behavior. There is an excellent introduction by Professor Roy Wood Sellars.

ERBLICHKEITSFORSCHUNG UND WIEDERGEBURT VON FAMILIE UND VOLK.

By Hermann Muckermann. *Herder und Co.*
Mk. 1.20 5 x $7\frac{1}{8}$; 66 *Freiburg*

The fourth edition of a little treatise on eugenics, for popular consumption. It follows entirely conventional lines. All the standard horrible examples are present and voting.

FARM POPULATION OF THE UNITED STATES. *An Analysis of the 1920 Farm Population Figures, Especially in Comparison with Urban Data, Together with a Study of the Main Economic Factors Affecting the Farm Population. Department of Commerce, Bureau of the Census Monographs VI.*

By Leon E. Truesdell.
Government Printing Office
$1.75 *Washington, D. C.*
7 x 10; xi + 536

Of interest as a source book to students of human biology generally, and to students of the population problem in particular.

FRÜHSCHEIN DER KULTUR. *Bilder aus Vorgeschichte und Urzeit.*

By Johannes Ledroit. *Herder und Co.*
4.80 marks *Freiburg im Breisgau*
$5\frac{1}{4}$ x $7\frac{3}{4}$; ix + 257

A brief popular account of man's development from paleolithic to iron age cultures. Not so good a book as several others in the same field.

AUF DER SPUR DES URMENSCHEN.

By Robert Lais. *Herder und Co.*
Mk. 3.50 *Freiburg*
$5\frac{1}{4}$ x 8; viii + 183 (paper)

Just another brief popular "prehistory," with no particular merit to recommend it above others in its class.

ZOOLOGY

LA VIE DES TERMITES.

By Maurice Maeterlinck. *Eugène Fasquelle*
12 francs $4\frac{3}{4}$ x $7\frac{1}{2}$; 217 (paper) *Paris*

A companion volume to *La Vie des Abeilles.* At the start Maeterlinck says that, being less young than when he wrote that book, it is even easier now than it was then to resist the temptation to depart from the exact scientific record in telling the story of the biology of termites. It is a charming book. But it is a little amusing to denizens of the Johns Hopkins University to be repeatedly told that L. R. Cleveland was enabled to carry out his important investigations on termites because of the wonderful resources of his laboratory at *Harvard* University!

BRITISH BIRDS. (*Volume IV*).

By Archibald Thorburn.
Longmans, Green and Co.
$5.50 6 x 9; x + 154 *New York*

This completes the popular priced edition of Thorburn's classic, previous volumes of which have been noticed in The Quarterly Review of Biology as they appeared. The orders represented in this volume are the Limicolae, Gaviae, Alcae, Pygopodes, and Tubinares. The plates are, of course, the great feature. The one for the woodcock in this volume is superb. But all are so good that it is really unfair

to pick out any particular one for special mention.

LES PIGMENTS DANS L'ORGANISME ANIMAL.

By J. Verne. *Gaston Doin et Cie.*
28 francs *Paris*
$4\frac{1}{2}$ x 7; xv + 603 (paper)

A thorough review of the present state of knowledge of animal pigments and their biological significance. There is a bibliography covering 43 pages, and a detailed index. The volume forms one number of the *Bibliothèque de Biologie Générale* edited by Professor Caullery, in the *Encyclopédie Scientifique*, of which other volumes have been noticed in these pages.

LES POISSONS ET LE MONDE VIVANT DES EAUX. *Études Ichthyologiques. Tome Premier. Les Formes et les Attitudes.*

By Louis Roule. *Librairie Delagrave*
30 francs $6\frac{1}{2}$ x 10; 359 (paper) *Paris*

Dr. Roule plans a monumental treatise on the natural history and biology of fishes, in nine volumes, of which this is the first. In it are discussed the general forms which fish take, long or short, fat or flat, flying or walking, etc. The book is well written, and illustrated with text figures and some 16 colored plates. It maintains a high standard of popular natural history writing.

THE INDIAN ZOOLOGICAL MEMOIRS ON INDIAN ANIMAL TYPES. I. PHERETIMA (*The Common Indian Earthworm*).

By Karm N. Bahl. *K. N. Bahl*
Rupee 1, annas 8 *Lucknow, India*
6 x $9\frac{1}{2}$; iv + 72

This is the first number in a proposed series of manuals of zoological types used in teaching in India. It gives a well-arranged, abundantly illustrated, and for class work quite sufficiently detailed account of the structural and functional anatomy of the earthworm.

MORPHOLOGIE DER TIERE IN BILDERN. *2. Heft. Protozoen; 2. Teil: Rhizopoden.*

By Alfred Kühn. *Gebrüder Borntraeger*
M. 18 *Berlin*
7 x $10\frac{1}{2}$; iv + 165 (paper)

This sample part suggests that the work as a whole will be a gorgeous zoological picture book, if other groups are treated in the same degree of detail that the rhizopods are. This number includes some 200 excellent drawings, with brief text, illustrating some 13 orders of rhizopods.

HADDOCK BIOLOGY. *III. Metabolism of Haddock and Other Gadoid Fish in the Aquarium. Fishery Board for Scotland Scientific Investigations. No. II.*

By Harold Thompson.
H. M. Stationery Office
2s. 6d. *Edinburgh*
$7\frac{1}{4}$ x $10\frac{3}{4}$; 14 + 4 plates (paper)

An interesting experimental study of the growth of the haddock, whiting, and codling in an aquarium, with a regulated and abundant food supply. The time rate of growth is increased by about 100 per cent over controls in the sea.

PLANKTON OF THE OFFSHORE WATERS OF THE GULF OF MAINE. *Bureau of Fisheries Document No. 968.*

By Henry B. Bigelow.
Government Printing Office
$1.25 *Washington, D. C.*
$7\frac{1}{2}$ x 11; 509 (paper)

This is the second part of the report on the oceanographic and biologic survey of

the Gulf of Maine. The first volume was noticed earlier in THE QUARTERLY REVIEW OF BIOLOGY. It is a monumental contribution to the subject of marine planktology.

COLLEGE ZOOLOGY.

By Robert W. Hegner. *The Macmillan Co.*
\$3.50 $5\frac{5}{8} \times 8\frac{1}{2}$; xxiii + 645 *New York*

In this revised edition of a standard, widely-used text the author has made considerable alterations in the arrangement of the material, and has added some seventy new illustrations.

TIERPFROPFUNG. *Die Transplantation der Körperabschnitte, Organe und Keime. (Die Wissenschaft. Bd. 75.)*

By Hans Przibram.
Friedr. Vieweg und Sohn
17.50 Rm. *Braunschweig*
$5\frac{1}{2} \times 8\frac{1}{2}$; viii + 303 (paper)

A thorough and comprehensive review of the zoological literature on grafting and transplantation, which will be useful as a reference work. There is an extensive bibliography, covering thirty-six pages, and a detailed index.

PRACTICAL ANATOMY OF THE RABBIT. *An Elementary Laboratory Textbook in Mammalian Anatomy.*

By B. A. Bensley. *P. Blakiston's Son and Co.*
\$3.00 $5\frac{1}{2} \times 8\frac{1}{4}$, 298 *Philadelphia*

The fourth edition of a well known and thoroughly established laboratory manual.

BOTANY

PHOTOSYNTHESIS.

By H. A. Spoehr. *Chemical Catalog Co.*

This is a thorough critical review of the present state of knowledge regarding photosynthesis. The material is discussed under the following heads: The origin of organic matter and the cosmical function of green plants; the nature of photosynthesis as determined by observations of gaseous interchange and the formation of organic matter; the products of photosynthesis; the methods of measuring photosynthesis; the chemistry of photosynthesis; energy relations; chlorophyll and the chloroplast. The book is extensively documented, but all references are given in extremely abbreviated form as foot notes. We believe that the usefulness of this excellent and much needed reference treatise would have been enhanced if all the references to the literature had been collected in a bibliography with complete citation of titles. There are detailed author and subject indices.

AIMS AND METHODS IN THE STUDY OF VEGETATION.

Published by The British Empire Vegetation Committee. Edited by A. G. Tansley and T. F. Chipp.
The Crown Agents for the Colonies
12s. 6d. $5\frac{1}{2} \times 8\frac{3}{4}$; xvi + 383 *London*

A useful handbook of methods used in plant ecology, designed to give actual and potential workers a statement of what is meant by the ecological study of vegetation, and of the reasons why it is important scientifically and of great practical value. Part I deals with methods in general, and with the broad environmental factors. Part II contains five essays on different regions, tropical, subtropical, arid, etc. Part III discusses types of vegetation. In Parts II and III the chapters are contributed by different special experts on the subjects covered.

LES FOUETS ET LE MOUVEMENT DES BACTÉRIES.
By Émile Frache. *Berger-Levrault*
$1.00 *Nancy*
$6\frac{1}{2}$ x 10; ix + 193 (paper)

The author of this extensive discussion of the morphology and physiology of bacteria strongly objects to the common usage which names the motor organs of bacteria "cilia" or "flagella." He wants these organs called "whips." The terminology seems relatively unimportant. What Dr. Frache has done is to make a thorough review of the literature, repeating many of the observations regarding the movements of bacteria and the organs by which they are produced. He seems to have contributed little that is new on his own account. There is a bibliography covering 16 pages, and four plates containing figures copied from the works of other bacteriologists.

OUTLINES OF THE HISTORY OF BOTANY.
By R. J. Harvey-Gibson.
The Macmillan Co.
$4.25 $5\frac{1}{4}$ x $8\frac{1}{2}$; x + 274 *New York*

An excellent general introduction to the history of botany, given originally as lectures to third-year students, by the professor in the University of Liverpool. It seems a pity that it is not illustrated, as the opportunity of useful and entertaining illustrations is so great in a general history of a branch of science, like this. There is a bibliography of 50 selected titles, intended merely as a guide to further reading in the field.

FOREST, STEPPE AND TUNDRA. *Studies in Animal Environment.*
By Maud D. Haviland (Mrs. H. H. Brindley) *The Macmillan Co.*

A chatty treatise on ecology, based primarily upon the author's visits to the desert tundras of Siberia in 1914, to the Steppes bordering the Danube in 1917, and to the forests of British Guiana in 1922. There is much material of general biological interest in the book. Two plates in black and white half tone to illustrate protective *coloration* are not very convincing.

THE CHEMISTRY OF CELLULOSE AND WOOD.
By A. W. Schorger.
McGraw-Hill Book Co., Inc.
$6.00 $5\frac{1}{2}$ x 8; xiv + 596 *New York*

While primarily a chemical treatise, the value of this book as a reference work to the botanist is enhanced by the fact that the author has kept in mind throughout that wood is a substance of biological origin. The literature is thoroughly reviewed, and there are detailed indices.

DIE ÖKOLOGISCHE MORPHOLOGIE DER PFLANZEN *im Lichte neuerer physiologischer und pflanzengeographischer Forschungen.*
By Hans Fitting. *Gustav Fischer*
1.80 marks *Jena*
$6\frac{3}{4}$ x 10; 35 (paper)

A critical review, documented with a bibliography of 68 references, of the present state of knowledge regarding the morphological effects of environmental forces upon plants, presented by the distinguished professor of botany at Bonn, as an address before the 1926 meeting of the German Botanical Society.

THE FERNS (FILICALES). *Treated Comparatively with a View to Their Natural*

rangiatae and Other Relatively Primitive Ferns.
By F. O. Bower. *The Macmillan Co.*
$10.00 7 x 10¼; 344 *New York*

A morphological treatise dealing with fifteen families of ferns, chiefly from the phylogenetic viewpoint, with abundance of illustration and bibliographic documentation. It sustains the author's high reputation for painstaking thoroughness.

AN INTRODUCTION TO PLANT ANATOMY.
By Arthur J. Eames and Laurence H. MacDaniels. *McGraw-Hill Book Co., Inc.*
$3.50 5⅞ x 9; xiv + 364 *New York*

An introduction to the descriptive morphology of plants, well written and illustrated. Each chapter is followed by a critically selected list of references to the literature.

PLANT PHYSIOLOGY. *Authorized Edition in English, Based on the German Translation of the Sixth Russian Edition and on the Seventh Russian Edition (1914) of the Textbook of Plant Physiology.*
By Vladimir I. Palladin, with additions and editorial notes by Burton E. Livingston.
P. Blakiston's Son and Co.
$4.00 6 x 9; xxxv + 360 *Philadelphia*

The third American edition of a standard botanical text. The chief changes are in the nature of additions to the text and notes by the editor. The continued success of the book is sufficient testimony to its merits.

OBSERVAÇÕES GERAES E CONTRIBUIÇÕES AO ESTUDO DA FLORA E PHYTOPHYSIONOMIA DO BRASIL. I. *Uma Excursão Botanica ao Norte de São Paulo e Regiões Limitrophes dos Estados de Minas e Rio de Janeiro. Realisada de 12 de April a 5 de Maio de 1926.*
By F. C. Hoehne. *Museu Paulista*
—— 9 x 12½; 55 (paper) *São Paulo*

This is a copiously illustrated account of a floristic-ecologic excursion in Brazil.

MORPHOLOGY

GRUNDRISS DER WISSENSCHAFTLICHEN ANATOMIE. *Zum Gebrauch neben jedem Lehrbuch der Anatomie, für Studierende und Ärzte.*
By Wilhelm Lubosch. *Georg Thieme*
M. 18 *Leipzig*
6⅝ x 9½; viii + 292 (paper)

The idea behind this interesting and valuable book is that the student of human anatomy is kept so busy learning the enormous collection of mere facts which he must know, that he has no time to learn, or even to think of, the broad biological significance of anatomy, or its philosophical meaning and relations to other sciences. In reasonable compass and in readable form this book aims to give him this general orientation. It succeeds admirably. Some enterprising American publisher ought to get out an English translation.

THE EMBRYOLOGY OF THE PIG.
By Bradley M. Patten.
P. Blakiston's Son and Co.
$3.50 6 x 9; ix + 323 *Philadelphia*

A text book of mammalian embryology for students of university grade. It is abundantly and very well illustrated. While the account centers about the pig embryo, because of its easy availability for class work, the intention is to use it only as a paradigm for mammalian de-

velopment generally. There is an excellently chosen and rather extensive bibliography, and a detailed index.

ZUR REFORM DER ALLGEMEINEN VERGLEICHENDEN FORMENLEHRE DER TIERE.

By E. Jacobshagen. *Gustav Fischer*
Mk. 4.50 $6\frac{1}{2} \times 9\frac{1}{2}$; 86 (paper) *Jena*

This volume is concerned with a discussion of the methodological and philosophical concepts underlying morphology, particularly homology.

PHYSIOLOGY

L'HERPÈS ET LE ZONA. "*Ectodermoses Neurotropes.*" *Étude Étiologique et Pathogénique.*

By C. Levaditi. *Masson et Cie.*
\$1.28 $6\frac{1}{4} \times 9\frac{1}{4}$; viii + 388 (paper) *Paris*

This volume represents the report on the nature of the virus of herpes that Levaditi was commissioned to make before the Congress of Dermatology and Syphilology held in Brussels in 1926. So authoritative and extensive a résumé of our knowledge will doubtless be received with great interest by all those workers who are now puzzling over the problems of herpes and its relationships to encephalitis lethargica. In his analysis, Levaditi takes up the infectious nature of herpes, the ways in which it can be transmitted to animals, the properties of the virus, the ways in which it usually gets into the body, the histologic appearances of the experimental lesions, the receptivity of the different tissues, immunity, and its mode of production. He concludes that many persons are carriers and that the virus takes effect when resistance is lowered. Certain strains of the virus of herpes apparently have a strong affinity for the tissues of the central nervous system, but there are many reasons for believing that they are not responsible for encephalitis lethargica. The two viruses are probably related but their elective affinities are different. There are many references to the Continental literature, and a few to American contributions. The book is fairly well illustrated, but there is no index.

MUSCULAR CONTRACTION *and the Reflex Control of Movement.*

By J. F. Fulton.

The Williams & Wilkins Co.
\$10.00 6×9; xv + 644 *Baltimore*

This is a comprehensive, thorough monograph *de motu animalium*, based largely upon the author's own researches, but with extensive review of the literature. The first part of the book deals with the physiology of the individual skeletal muscle fibre, and the second part with integrated muscular action in bodily movements and postures. The whole is a contribution to physiology of the first rank. The book is extensively illustrated, contains a bibliography of 1066 titles, and author and subject indices.

THE LYMPHOCYTE IN RESISTANCE TO TISSUE GRAFTING, MALIGNANT DISEASE, AND TUBERCULOUS INFECTION. *An Experimental Study. Monographs of The Rockefeller Institute for Medical Research. No. 21.*

By James B. Murphy.

The Rockefeller Institute for Medical Research
\$2.00 $6\frac{3}{4} \times 9\frac{7}{8}$; 168 (paper) *New York*

In this monograph Dr. Murphy brings together, in a connected whole, the results of the investigations which have been carried on in his laboratory during

the past fourteen years, on the function of the lymphocyte as a defense mechanism of the organism, particularly with reference to malignant tumors. It is of great service to have this valuable work available in a single volume. It is an important contribution to the cancer problem.

DIE DREI-DRÜSENTHEORIE DER HARNBEREITUNG.

By August Pütter. *Julius Springer*
Rm. 9.60 *Berlin*
$6\frac{1}{4} \times 9\frac{5}{8}$; v + 173 (paper)

The "three glands" of the kidney, according to Pütter's view, are: (a) the "nitrogen glands" of the *tubuli contorti*, (b) the "water glands" of Bowman's capsule of the glomeruli, and (c) the "salt glands" of the thickened shank of Henle's loop. He presents a mass of experimental and observational data, both personal and derived from the literature, in support of the view that by the combined action of these "glands," the known activities of the kidney can be explained.

RECENT ADVANCES IN PHYSIOLOGY. *Second Edition.*

By C. Lovatt Evans.
P. Blakiston's Son and Co.
$3.50 *Philadelphia*
$5\frac{1}{4} \times 8$; xiii + 370

This excellent little book, which was enthusiastically recommended in The Quarterly Review of Biology when it appeared, has already passed into a second edition. The chief alterations have to do with thyroxin and insulin. We again commend it to all biologists as a most entertaining and lucid account of present activities in the field of physiology.

ACTIONS AND USES OF THE SALICYLATES AND CINCHOPHEN IN MEDICINE.

By P. J. Hanzlik.
The Williams & Wilkins Co.
$3.50 6 x 9; xiii + 200 *Baltimore*

On account of the large amount of research work that Hanzlik has done on the salicylates he comes well prepared to the discussion of his subject. His book will be of great interest, not only to pharmacologists, but to all those clinicians who are concerned with the problems of treating arthritis. The reviewer, a clinician, found it easy to read it from cover to cover.

DIE HÖCHSTE NERVENTÄTIGKEIT (DAS VERHALTEN) VON TIEREN. *Eine zwanzigjährige Prüfung der objektiven Forschung bedingte Reflexe.*

By J. P. Pawlow (Translated by G. Volborth).
J. F. Bergmann
RM. 24 *Munich*
$6\frac{3}{4} \times 10$; xi + 330 (paper)

It is a useful contribution to the literature to have collected in one volume, and in a language more widely known than Russian, the scattered original papers, lectures and addresses of Professor Pawlow on conditioned reflexes and related aspects of the physiology of the central nervous system. The book unfortunately has only three illustrations, and no subject index.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 216.* Containing following articles: *Die Luftcalorimetrie*, by Max Rubner; *Eine Methode der Calorimetrie kleiner Tiere*, by Richard Wagner; *Der Kestnersche Respirationsapparat für kleine Tiere*, by Franz Groebbels; *Die Calorimetrie*, by W. Klein and Marie Steuber;

Graphische Stoffwechselregistrierung, by Erich Leschke; *Die Respirationsapparate für Menschen des Physiologischen Institutes Hamburg*, by Otto Kestner; *Über die Verwendung von Masken zur Bestimmung des respiratorischen Gaswechsels*, by Hermann v. Schroetter.

Urban und Schwarzenberg
Mk. 6 7 x 10; 117 (paper) *Berlin*

It is the first three of the contributions in this number of the Abderhalden handbook which will chiefly interest general biologists. The later sections are for the human physiologist.

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 209. Die radioaktiven Substanzen*, by Stefan Meyer. *Bestimmung der Verbrennungswärme und ergänzende thermochemische Messungen*, by A. W. Roth. *Urban und Schwarzenberg*
Mk. 7.80 7 x 10; 153 (paper) *Berlin*

This number of the Abderhalden handbook is chiefly of interest to the biophysicist. The discussion of both radioactive substances and thermochemical measurements is primarily physical in the technical sense.

BIOCHEMISTRY

RECENT ADVANCES IN BIOCHEMISTRY.
By John Pryde.
P. Blakiston's Son and Co.
$3.50 *Philadelphia*
$5\frac{1}{4}$ x 8; viii + 348

This is a companion volume to Lovatt Evans' excellent little treatise in the "Recent Advances" series. While perhaps of smaller general biological interest than that book, it is nevertheless a sound and useful piece of work. The subjects reviewed are: Protein catabolism; amino acids and urea; colloids; nucleo-proteins; carbohydrates; fats; phosphorus compounds; sulphur; vitamins; haemoglobin; specific immunological reactions; and chemotherapy.

DER HEUTIGE STAND DER CHEMOTHERAPEUTISCHEN CARCINOMFORSCHUNG.
By N. Waterman. *Julius Springer*
Rm. 6.60 $6\frac{3}{4}$ x 10; 74 (paper) *Berlin*

A review of the literature with the presentation of original data regarding the biochemistry of malignant tumors, with special reference to their therapeutic treatment with ions of the metals. There is a bibliography covering over two pages.

INTRODUCTION TO PHYSIOLOGICAL CHEMISTRY.
By Meyer Bodansky.
John Wiley and Sons, Inc.
$4.00 $5\frac{3}{4}$ x 9; vii + 440 *New York*

An excellent condensed text, by the associate professor of physiological chemistry in the University of Texas. Abundant bibliographical citations are given in footnotes.

LEHRBUCH DER PHYSIOLOGISCHEN CHEMIE.
By Olof Hammarsten, with the collaboration of S. G. Hedin, J. E. Johansson and T. Thunberg. *J. F. Bergmann*
29.40 RM. *München*
$6\frac{3}{4}$ x 10; viii + 835 (paper)

The eleventh edition of the standard text book of physiological chemistry. The chapter on metabolism and nutrition has been entirely rewritten on a new plan,

while other chapters have been brought up to date.

PRACTICAL COLLOID CHEMISTRY.
By Wolfgang Ostwald, with the collaboration of Dr. P. Wolski and Dr. A. Kuhn. Translated by I. Newton Kugelmass and Theodore K. Cleveland. *E. P. Dutton and Co.*
$2.25 $5 \times 7\frac{1}{4}$; xvi + 191 *New York*

The fourth edition of this widely used laboratory manual, considerably revised, and with fifteen new experiments added.

SEX

SEX IN MAN AND ANIMALS.
By John R. Baker. *Alfred A. Knopf, Inc.*
$3.00 $5\frac{1}{2} \times 8\frac{5}{8}$; xvi + 175 *New York*

A brief popular account, for the general reader, of the present status of biological knowledge regarding sex. The topics treated are: The biological significance of sexual reproduction, sex characters and sexual selection; sex chromosomes; sex hormones; abnormalities of sex; hermaphroditism; parthenogenesis; sex ratio; control of sex; sex behavior. The book is well written, but no harm would have been done by *naming* some more of the biologists whose investigations made it possible for Mr. Baker to write this book. After all the investigators who furnish the raw material from which writers of popular science compose their delicious confections are actual persons, lowly though their status be. Who knows but that they might be spurred on to even nobler efforts by a little personal recognition?

[*Editorial Note:* Lest there be any misunderstanding we think it wise to say that the writer of this notice has never worked in the fields of biology discussed by Mr. Baker.]

THEORIES REGARDING THE DETERMINATION OF SEX AND THE POSSIBILITIES OF SEX CONTROL.
By Nils O. Lundell. *Nils O. Lundell*
—— *608 Broadway, Far Rockaway, N. Y.*
6 x 9; 10 (paper)

The author, who is a practising physician graduated from Cornell University Medical College in 1911, claims "that it is possible to examine the maternal and paternal bloods in early pregnancy and tell what the sex of the offspring will be; also that examination of these bloods prior to conception will tell what the sex will be if impregnation takes place and further that we can control the sex when dealing with normal healthy individuals and sex organs."

He then presents an affidavit to the effect that in "over one hundred cases" he "foretold what the sex would be and made no errors." Unfortunately he omits anywhere to state just how the trick is turned.

THE REPRODUCTION OF LIFE. *A Handbook of the Science of Reproduction in Nature and Man.*
By A. J. Cokkinis. *Wm. Wood and Co.*
$3.50 *New York*
$5\frac{1}{4} \times 8\frac{1}{4}$; xvi + 287

An excellent elementary account, with abundant illustrations, of the general biology of reproduction in plants and animals including man. There is a refreshing absence of moral precepts. The book is just plain, unadorned biology, stated clearly and in simple language.

HAPPINESS IN MARRIAGE.
By Margaret Sanger. *Brentano's*
$2.00 $5\frac{1}{4} \times 7\frac{1}{2}$; 231 *New York*

A *vade-mecum* for newlyweds, written

with charm, insight, and a refreshing absence of pseudo-scientific slush by way of rationalization. The sound central idea of this book is that the kind of activity which constitutes the sole reason for a male bee's existence can be made a very pleasant pastime.

SEX HYGIENE. *The Anatomy, Physiology, and Hygiene of the Sex Organs.*
By Julia Kinberg-von Sneidern and Alma Sundquist. Translated by Mary E. Collett.
Henry Holt and Co.
\$1.75 $5\frac{1}{4}$ x 8; 114 *New York*

A brief, sensible treatise on the personal hygiene of sex. The Swedish original first appeared fifteen years ago, and has met with success as a supplement to biological texts used in secondary schools.

MAN AND WOMAN. *A Study of Human Secondary Sexual Characters.*
By Havelock Ellis. A. and C. Black, Ltd.
10s. 6d. *London*
$5\frac{1}{2}$ x $8\frac{1}{2}$; xxiii + 563

The sixth revised edition of a well known treatise. It is a useful work of reference, which fortunately carries no obligation to the reader to agree with all the conclusions.

BIOMETRY

INTERPOLATION.
By J. F. Steffensen.
The Williams & Wilkins Co.
\$8.00 6 x 9; ix + 248 *Baltimore*

This is a technical mathematical treatise, which covers with great thoroughness and detail the subjects of interpolation, quadrature, numerical differentiation and integration, etc. It will be found a valuable reference work by the advanced biometrician.

PSYCHOLOGY AND BEHAVIOR

THE ADVENTURES OF A LION FAMILY *and Other Studies of Wild Life in East Africa.*
By A. A. Pienaar. Translated from the Afrikaans by B. and E. D. Lewis.
Longmans, Green and Co., Ltd.
\$1.65 $4\frac{3}{4}$ x $7\frac{1}{4}$; xv + 256 *New York*

A most entertaining book, written by a young Dutch South African. It embodies three stories, based upon his observations in the field as a hunter and amateur naturalist. The bulk of the book is made up of the story of a family group of lions. The second story is unimportant. The last concerns the adventures of a rhinoceros and a hippopotamus, who started an association with each other when they were left as orphans at the same time through the activity of hunters, and fought the battles of life together until one of them was killed by a poisoned spear.

By some this book will be instantly branded as arrant nature-faking. Perhaps it is. But anyhow it is only fair to let the witness be heard. The author says:

> Imagination plays no part in the following sketches of animal life. The writer has simply endeavoured to reproduce the habits and life of the wild creatures which he has learnt to know during the course of many a year. Among wild animals there also exists a kind of spiritual life which often fills the attentive observer with wonder. After a while it becomes possible for him to comprehend their sensations from their outward behaviour.
>
> In the sketch, "The Two Friends," where the action proceeds for a long period and in changing scenes, the writer has incorporated various incidents

in one tale; yet in the smallest particular it rests upon observations that are absolutely true to Nature, and upon personal experiences.

In the "Adventures of a Lion Family" the occurrences—with the exception of parts of the last chapter—are written down almost literally as they happened.

The scenery in which the animals are depicted is in every detail drawn from Nature.

Just a little while before we read this book we waded through a long and preternaturally dull account of an investigation of the habits of an invertebrate that shall be nameless, by a serious, indeed a very serious, student of animal behavior, who had been brought up in the notion that he must never read into the behavior of an animal any anthropopsychism. The net result of this careful investigation was simply to prove that the author was an idiot, and to leave the state of real knowledge of the animal about where it was before. If this kind of painstaking nonsense is to be regarded as science and Pienaar's real insight is to be branded as imagination, God will presently have to take even greater pity on erring mortals than he so far has.

THE MIND OF A GORILLA. *Genetic Psychology Monographs, Vol. II, Nos. 1 and 2, By Robert M. Yerkes.* *Clark University*
$3.00 *Worcester, Mass.*
6 x 9; 193 (paper)

This is an extraordinarily interesting book. It recounts the author's experiences with Congo, a young female gorilla. Her owner, Mr. Ben Burbage, gave every opportunity, at his home in Florida, for the observational and experimental study of her behavior. In some respects this seems to us the best piece of work Yerkes has ever done in his long and distinguished career as a comparative psychologist. At its high points it seems to achieve real insight into the mind of this charming female, who is plainly no fool, but on the contrary, within certain limitations, a highly intelligent creature. Given a parallel set up, in the two important respects that no communication by language was possible, and that the environmental conditions and the experimental demands were totally different from those encountered in the natural course of existence, we suspect that many a stenographer would give less evidence of intelligence, as an experimental subject, than did Congo. He is a dull clod who will not be thrilled by this book. We eagerly await further reports about Congo.

MYTH IN PRIMITIVE PSYCHOLOGY. *By Bronislaw Malinowski.*
W. W. Norton and Co., Inc.
$1.00 $4\frac{1}{4}$ x $6\frac{1}{2}$; 94 *New York*

The distinguished author presents detailed evidence from his wide field experience as an anthropologist, in support of the thesis that:

Myth, as a statement of primeval reality which still lives in present-day life and as a justification by precedent, supplies a retrospective pattern of moral values, sociological order, and magical belief. It is, therefore, neither a mere narrative, nor a form of science, nor a branch of art or history, nor an explanatory tale. It fulfils a function *sui generis* closely connected with the nature of tradition, with the continuity of culture, with the relation between age and youth, and with the human attitude towards the past. The function of myth, briefly, is to strengthen tradition and endow it with a greater value and prestige by tracing it back to a higher, better, more supernatural reality of initial events.

Myth is, therefore, an indispensable ingredient of all culture. It is, as we have seen, constantly regenerated; every historical change creates its mythology, which is, however, but indirectly related to historical fact. Myth is a constant by-product of living faith, which is in need of miracles; of sociological status, which demands precedent; of moral rule, which requires sanction.

LE FONDEMENT PHYSIOLOGIQUE DES INSTINCTS DES SYSTÈMES NUTRITIF, NEUROMUSCULAIRE ET GÉNITAL.

By Bjorg-Caritas Thorlakson.

Les Presses Universitaires de France

20 francs *Paris*

$5\frac{1}{2} \times 9$; 393 (paper)

An interesting philosophical essay by an Icelandic author, which attempts to arrive at a rational picture of the biological basis of instincts. His theory is essentially holistic (*sensu* Smuts). It may be put as a formula in this way. The synthesis aptitude (= in part at least appetite) + function + structure is at the same time a morphogenetic and an instinctive-genetic synthesis. The argument is well documented from a rather wide knowledge of general biology and physiology.

ON THE MELODIC RELATIVITY OF TONES. *Psychological Monographs. Vol. XXXV, No. 1.*

By Otto Ortmann. *Psychological Review Co.*

—— *Princeton, N. J.*

$6\frac{5}{8} \times 9\frac{3}{4}$; 47 (paper)

A valuable contribution to the psychology of music. Perhaps the most interesting conclusion, which is supported by sufficiently extensive statistical data, is that the melodic relationship of tones is based upon pitch-proximity, with which it varies directly.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

LES NÉOPLASMES ET LEUR THÉRAPEUTIQUE MÉDICALE.

By Ed. Baronaki. *Norbert Maloine*

12 francs *Paris*

$5\frac{5}{8} \times 7\frac{1}{2}$; 137 (paper)

The author of this treatise, who is an honorary surgeon of the *Hôtel-Dieu* at Blois, believes that cancer has its inception in a disturbance of the endocrine balance, and that the way to treat malignancy is by injecting a substance which he calls "Neoplastine," which is a colloidal, "plasmatic" solution containing a mixture, in unspecified proportions, of the salts of calcium, magnesium, phosphorus, potassium and sodium, associated with thyroid and suprarenal extracts. Besides this some rather wonderful "cachets" are exhibited, which are said to contain, again in unspecified proportions, diastatic and tryptic ferments, oxyhemoglobin and lecithin, and soluble salts of lime and soda. According to 20 case histories, given at the end, the treatment leaves little to be desired. But before the work is accepted at its face value it would be well to have an independent investigation of its merits, presuming that Dr. Baronaki is prepared to disclose the details of the composition of his medicines.

RELATIVITY IN MAN AND SOCIETY.

By Arthur F. Bentley.

G. P. Putnam's Sons

\$3.00 *New York*

$5\frac{1}{2} \times 8\frac{1}{4}$; xix + 363

What worries Mr. Bentley is the ambiguity of words, particularly words used in discussions of psychological and sociological matters. For example, he thinks that what the rest of us call "sociology" would be better called "man-society." And since this is the main subject that he wants to talk about he feels it essential to discuss a lot of other words which undeniably get us all into trouble.

Thus: "Let us take a social fact or fact-complex, any one. Take the Volstead Law, federal prohibition of alcoholic drinks. What do we have? A set of words, an enacting clause, many printed

copies. When we have said that, have we said anything?"

To which rhetorical question a joyful shout arises in the Maryland Free State, NO-O-O-O!

The relation of Einstein to all this seems to be precisely that which King Charles' head had to the meditations of Mr. Dick.

THREE LECTURES ON ATOMIC PHYSICS.

By Arnold Sommerfeld. Translated by Henry L. Brose. *E. P. Dutton and Co.*
$1.00 $4\frac{3}{4} \times 7\frac{1}{4}$; 70 *New York*

This little book has nothing directly to do with biology. The lectures deal with recent developments of the quantum theory. But the biologist nowadays ought at least to have some notion of the extraordinary goings-on in physics, for some of the modes of thinking now current in that science are of a sort with which the biologist has long been familiar (cf. Whitehead for example). In our youth we were not accustomed to meet such statements as the following from the book under review (p. 7), in a technical treatise on physics. "We have a 'phylogenetic principle' for atoms just as much as in biology."

THE NEW SCIENCE OF RADIENDOCRINOLOGY IN ITS RELATION TO REJUVENATION AND THE RELIEF OF COMMON AILMENTS. *Based on the Radiation Technique of Dr. Eugen Steinach of Vienna.*

By One of America's Foremost Radiendocrinologists. *Medical Science Publishing Co.*
$1.00 $4\frac{1}{2} \times 6\frac{1}{8}$; 64 (paper)

Abrams may be dead but his ions still go marching on. "The Radiendocrinator is an extremely complex apparatus, despite its small size and apparent simplicity of construction. Yet it is not difficult to comprehend the basic principle by which it operates." This is the only description of the apparatus to be found. But truly the basic principle on which it operates is *not* difficult to comprehend. It is that fundamental physical principle, technically known as *gullibility*.

ÉDUCATION, SCIENCE, PATRIE.

By Lucien Poincaré. *Ernest Flammarion*
10 francs *Paris*
$4\frac{1}{2} \times 7\frac{1}{2}$; 246 (paper)

A posthumous collection of popular essays and public addresses dealing with educational problems and patriotism. It is beautifully written by a master of the French language. But it is dubious whether any useful purpose will be served by the preservation of material of such ephemeral significance.

DER CHRISTLICHE MONISMUS. *Zeitgemässe Betrachtungen über christliche Glaubenswahrheiten.*

By Erich Wasmann. *Herder und Co.*
Mk. 2 *Freiburg*
$4\frac{1}{2} \times 6\frac{7}{8}$; xii + 105

A pious tract which has nothing to do with myrmecophily or with any other branch of zoology. Its purpose seems to be primarily to strengthen the faith of those who have it, and perhaps snare a sinner here and there and fetch him into the fold. But it has nothing to do with biology. It is a *very* pious book.

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THE QUARTERLY REVIEW *of* BIOLOGY

PHYSIOLOGICAL ONTOGENY

I. THE PRESENT STATUS OF THE PROBLEM

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INTRODUCTION

EVERY pattern in nature has its own intrinsic set of properties, and the correlation of the two—patterns and properties—is an interest germane to science. It is of particular consequence when it involves a progressive sequence of correlations in a system characterized by unstable dynamic equilibria. In biology this would be the case for the series of organic changes in the life span of an individual being. It is the purpose of these investigations to discover relationships between the structure and the behavior of an organism as functions of age. The subject may be divided into two parts—namely, a study of (1) the modifications of form, and by this is meant the chemical constitution as well as the gross and microscopic structure, and (2) the changes in function. Thus two age old problems in consequence are involved: (1) the relationship of structure and behavior and (2) the problem of aging.

It is suggested that life is an irreversible process and that every organism of whatever species, as a whole or in any of its parts, being what it is and having the properties which it seems to have, will tend to exhibit similar fundamental manifestations and dispositions in the processes of growth, differentiation, and senescence. In other words it is assumed that within limits there is an essential order in all kinds of evolution.

In a world of great complexity, the attention of man is turned with relief to the more determinate limits of life, creation and death. The very definiteness of such points heightens the sense of reality. Death, in particular, is characterized by a finality which seems decisive. But death is only the end point in a long chain of events, and biologically it may be best understood in terms of the antecedent physico-chemical processes.

Although life, as a concept, has never been given a definition satisfactory to all biologists, there has been considerable unanimity about the ultimately significant characteristics or properties of living matter, common to all its forms. These prop-

erties have not, however, been systematically measured in terms of age, although it is obvious that time is a dimension which should not be neglected in any physiological outlook.

For biological science we believe there is no greater task confronting its disciples than the formulation of a concept that will adequately describe the progress of life itself. Since the earliest times it has been recognized that there is an order in nature and that this order is not a static condition but a dynamic "becoming" in which similar events seem to recur in a more or less periodic fashion. The life of an individual may be considered as a definite cycle with a beginning and an ending. If special attention is given to the functional aspects, the study may properly be called physiological ontogeny. Later, physiology may be correlated with morphology. One may deal with the whole organism or with a particular system.

Attempts have been made in the past to ascribe death to the senescence of some one organ. Such a point of view, however, does not change the general problem, even though it might lead one to concentrate attention upon a particular part. It is safe to suppose that if this special part could be prevented from undergoing morbid change, death would occur as a result of aging in some other organ, for the viability of the total organism depends upon the coördinated activity of its integral parts. It may be assumed, therefore, for theoretical purposes that natural death coincides with the simultaneous cessation of activity in all the cells of the body, even though it is recognized that in any one case this probably never occurs.

Keith Lucas, referring to physiological evolution, a subject that he considered of the first magnitude, emphasized the importance of investigating differences in functional capability rather than normal behavior, or in other words, the behavioristic differences that could be brought out under special experimental conditions. Lucas called it "the primary problem of comparative physiology—a problem whose investigation is wholly necessary for the understanding of the evolutionary process. It may be stated in general terms as the question to what extent and along what lines the functional capabilities of animal cells have been changed in the course of evolution."

Before discussing the methods of investigation and the results of our preliminary studies in physiological ontogeny it would be well to review the available relevant facts and the various hypotheses that have been advanced to describe them.

BIOLOGY

The chief facts pertaining to the phenomenon of aging, of which there are a great variety, have been derived from investigations upon the lower forms of life. It is not a simple matter to estimate them. A review of the literature discloses many apparently irreconcilable contradictions. The difficulty is due to the customary practice of each observer of focussing his attention upon a single part only of the multiformity of organic change, and even in some instances of proposing the specially selected factor as the "cause" of senescence. Few of the observations may, moreover, be correlated one with another, since they deal with different species or with the same species over different periods of the life span. To arrive at a comprehensive view of the developmental process a more systematic treatment involving the simultaneous analysis of numerous functions over the same developmental cycle is required.

It is now generally agreed that unicellu-

lar organisms and perhaps any tissues in the body of the metazoan when freed from the organizing or integrating forces of their own milieux are potentially immortal. Under experimental conditions when the environment, as for instance culture media, whether of tissue cells or of bacteria, is regularly refreshed, growth continues indefinitely and at a continuous rate theoretically, that is to say by geometrical progression. The experiments of Woodruff with paramecia, Carrel with fibroblasts, Leo Loeb with transplanted tumors, and Felton with bacterial microorganisms are perhaps the most convincing of such researches. In a state of nature, however, eventually the increase in numbers causes congestion, and in consequence competition for available nutriment. Regularly then as the food supply becomes inadequate some of the less adapted or adaptable individuals die without division and the growth rate of the colony declines and eventually comes to a dead level. In both instances, either under experimental or under natural conditions, the individuals of the colony show evidences of growth, differentiation, and senescence, followed by division and rejuvenescence, but in the former state where there is no limit to growth the two processes of differentiation and dedifferentiation may balance each other so that with time there is no predominance of differentiation, whereas in nature it is possible that a "slow progressive senescence may occur extending through many generations" (Child). With a limited quantity of food, however, such as in an untransplanted bacterial culture all the living cells eventually die. A condition such as this is somewhat similar to the state of affairs in a single multicellular organism which may be viewed as a colony of cells the environment (that is to say internal environment) of which is continually undergoing alteration and becoming less fit. The former (colonies of bacteria) may be used as examples of phylogenetic or racial, the latter (metazoa) of ontogenetic or individual senescence and death. In both cases there is that reciprocal dependence. The active constituents progressively modify their immediate surroundings, and the latter in turn modify the velocity and nature of the vital functions. In the case of racial growth the degradation of activity may be remedied by experimental revivification of the environment. In the metazoa the existence and nature of their organization prevent this. It seems to depend upon the dominance of what might be termed spheres of control, so that except under abnormal or artificial conditions (as for instance in the case of neoplasms and tissue cultures) the cells do not and cannot escape from their own progressively deteriorating environment.

The distinction between the protozoa and the metazoa on the basis of immortality is, however, somewhat misleading, because even under natural conditions the sex cells of the metazoa are potentially immortal. From this point of view the soma may be regarded as a mere appendage—highly differentiated, but affording temporary lodging only for the immortal germ plasm, and destined to be periodically destroyed and renewed in the interests of the race.

Our own interests are concerned not with racial evolution but with the analogous phenomenon, individual evolution. A unicellular organism in its interdivisional period, of course, might be suitably included for study. Each individual protozoon grows, ages, and differentiates, and then either dies or rejuvenates by division; for senescence, but not death, is a phenomenon characteristic of all living matter. It has been observed that with

the growth of a protozoon there is an agglutination of solid material, a formation of metaplastic elements, together with a decrease of surface energy and of osmotic pressure, but as there is no available systematic quantitative treatment of such phenomena during the interdivisional period we may without further delay turn to data from metazoan investigations.

Changes with time may be conveniently divided into those of (1) matter and (2) energy. Under the former heading may be included both growth and form. Changes in form may be observed by a study of gross and microscopic structure, and by the method of chemical analysis. The latter, that is to say changes in energy or function, would include modifications occurring in the natural life history of the organism and also the change with age in reactivity, quantitatively or qualitatively considered, when the organism is subjected to environmental stress, infectious organisms, or untoward experimental procedures. Of course such a division into matter and energy, though convenient, falsifies nature by its arbitrariness. We may profitably recall John Hunter's dictum that "structure is only the ultimate expression of function," or Professor William Wheeler's phrase "form is the excretion of function."

Changes in matter

Growth. Since the time of Quetelet, growth or increase in mass, and form or the result of differential growth in various directions, both as functions of time, have been made the object of numerous statistical studies. (The subject has been treated comprehensively in Professor D'Arcy Thompson's admirable book.) The growth process has not been analyzed, however, so that either the quality of the growth may be known or what seem to be different phenomena (for instance "selective absorption," which involves biological concepts, and osmotic effects, which may be described by physicochemical laws) may be separately apprehended. One must, therefore, use the term in a vague sense to connote the resultant of forces, that is to say the increase in total volume or mass under relatively normal conditions.

It seems that in man, as probably in other species, there are three chief "cycles" of growth. Robertson, who has studied this phase of the subject and has recently summarized the data in a comprehensive fashion, differentiates the following three periods of accelerated anabolic activity: (1) the infantile, with its peak during the latter part of fetal and early months of extra-uterine life; (2) the juvenile, comprising the third, fourth, and fifth years of life; and (3) the adolescent, which occurs at puberty.

The weight curve has in consequence not a simple form. Numerous attempts have nevertheless been made to represent volume, weight, and other dimensional values by single even if not simple mathematical equations with time as the variable. It has not been possible to express the entire span by any rational equation, but by choosing certain phases of it, relatively simple expressions have been found which would fit the portion of the curve selected. Loeb, Ostwald, and Robertson were originally interested in this aspect of the subject and developed conceptions based on the view that growth is an autocatalytic reaction. Later Loeb abandoned the idea, but Robertson carried it into greater detail and elaborated a theory which states that growth rate is determined by a "master reaction" of the order of a monomolecular autocatalytic reaction; this, being the slowest of perhaps a long chain of reactions, governs the rate of all other transformations. The most

recently reported measurements of growth, the results of which have been interpreted by this theory, are those of Brody.

All the objections which arise relative to the autocatalytic hypothesis cannot be enumerated at the present time. No distinction in the theory is made between the growth of a colony of unicellular organisms in unchanged culture medium and that of a single individual, both of which give *S*-shaped curves when the total weight is plotted against time. If growth is expressed in terms of percentage increase in mass, however, the important distinction between phylogenetic and ontogenetic growth is made evident. Colony, racial, or phylogenetic growth (as in the case of bacteria and paramecia), after a short latent period in the presence of an experimentally modified environment, proceeds at a constant rate (compound interest law). The individual organism, on the other hand, instead of maintaining a constant growth rate shows from the beginning considerable negative acceleration, a fact to which Minot was the first to call attention.

The principal objection to the autocatalytic growth law, however, is that it disregards chemical differentiation. It commences by erecting the concept of a "master-reaction," monomolecular in nature, which determines the velocity of organic growth. Since it is obviously impossible to measure the velocity of a reaction, the components and products of which are unknown, the total body weight is taken to represent the result of all the reactions involved, and in this manner the velocity of the theoretical master-reaction. This step depends for its validity upon the assumption that there is a constant direct proportionality between the two, that is to say between the total body weight and the mass of the product; an assumption that is obviously unwarranted.

In view of the facts relative to chemical differentiation it is difficult to see how any equation to describe such an infinitely complicated process as growth could have more than statistical significance. In fact dry weight would seem a better criterion of growth than wet weight. For the water in the body may be considered as essentially passive, and the very marked changes with age in its concentration are obedient to significant redistributions and spatial changes amongst the chemical constituents of the protoplasm.

Form. Gross structures. Into a description of the development of specialized parts and of organs we need not enter. This subject has been exhaustively treated in embryological textbooks. The chief gross structural developments as far as the heart—an organ in which we have been especially interested—is concerned are: (1) the separation of auricles and ventricles with the development of valves, (2) the partition into right and left hearts by means of the interventricular and interauricular septa, and (3) the establishment of connections with the central nervous system together with the development of nodal points and a conducting mechanism for the transmission of excitatory impulses. It is commonly assumed that growth and differentiation, both of the whole and of its parts, proceed synchronously. This is unwarranted, for no attempts have been made to measure the velocity of the change in form.

There are facts, however, which indicate that growth and differentiation under certain conditions have a negative correlation. Excessive exposure to light for instance generally retards the growth of plants but may lead to premature differentiation; and conversely growth may proceed at night with the greatest velocity, but the deficiency in illumination may completely inhibit differentiation. Again, the investigations of Gubernatsch,

Cotronei, and Romeis have shown that thyroid gland feeding accelerated differentiation in tadpoles but stunted growth; whereas the effect of feeding thymus gland was the reverse. Morse showed that the action of thyroid gland could be duplicated with iodized amino-acids.

Microscopic structure. Morphologists who have become interested in the problem of aging have for the most part limited themselves to a description of cytological changes such as calcification and pigment formation, characterizing such formation as the cause or the concomitant of old age. But other characterizations of the changes have been proposed. Hodge and Minot called attention to the decrease in the ratio of nucleus to cytoplasm with age. The latter laid the most particular emphasis upon this point and believed it to be the crux of the problem. He did not, however, discover the rate at which this ratio changed with age, nor did he correlate it with other functions to make evident the dependence of one upon the other. His results were later contradicted by the work of Richard Hertwig, who believed on the contrary that the nucleoplasmic ratio increased with age. These histological findings no longer interest us much because of our awareness of the inadequacy of the fixation and staining methods employed to demonstrate the presumed relationship. Recently Le Breton and Schaeffer have used the ratio of purine and non-purine nitrogen as the criterion of the nucleocytoplasmic ratio and, granting the validity of the assumed correlation, have by this method come upon a quantitative measurement of a structural relationship. Their data showed that in chicken embryos the nucleo-cytoplasmic ratio decreased markedly with age.

The accumulation of so-called metaplasmic granules in the cytoplasm has been observed by numerous workers. It is apparent that such elements, hypothetically inert, would mechanically obstruct the passage of molecules and thus decrease the rate of chemical change. Mühlmann, Minot, Hodge, Kassowitz, Conklin, and others have described somewhat similar accretions. Under this head may be classed the lipoid granules in the central nervous system, and the brown pigment in the heart and liver. These and similar histological studies have not been, and cannot hope to be, productive of important results in the search for the chief factors in the mechanism of senescence, unless they are correlated in a more or less systematic fashion with function. In considering changes with development in the cytological aspects of heart muscle the chief points of interest are (1) the changes in composition and in structure of the muscle fiber both in the course of normal growth and in the case of such abnormal growth as is exhibited in hyperplasia and hypertrophy, (2) the history and apparent rôle of elastic tissue, (3) the establishment of nodal centers and (4) the organization of the conducting system. These subjects have been reviewed in a separate chapter in Cowdry's *Special Cytology*.

Chemical constitution. Although a considerable amount of data has been accumulated regarding the chemical constituents of the body of the same and different species at successive periods of the life span, it has yet to be organized into an intelligible form or correlated either with morphological or physiological knowledge. Analyses by Bezold, Liebermann, Weigert, Fehling, Michel, Donaldson, Hatai, and others have taught us that with development there is progressive desiccation of the tissues with a consequent rise in the concentration of nitrogen, fat, and total ash. The ratio of fat to nitrogen also appears to increase with age.

The most comprehensive compilation of data was made by Aron in 1913 and extended in 1921. He included figures for water, nitrogen, fat, and many of the inorganic substances. More recently Moulton has added somewhat similar analyses for swine and cattle. Méndeléef has presented figures which show a gradual rise of the serum pH in guinea pigs during the embryonic and early infantile period, but as the technique, which in this instance is all important, was not described and since some of our own experiments gave opposite results, that is to say a fall in pH with age, one must suspend judgment on this point. Embryonic blood sugars estimated by Aron were variable and difficult to interpret in relation to age. Riddle and Honeywell found no differences in the concentration of blood sugar in pigeons of different ages. (Compare with this the data in human individuals given later.) In most cases the available estimates lack precision and are hardly adequate for further calculations or theoretical treatment.

It would naturally be an error to believe that chemical analyses will yield the basis for constructing the whole picture of physico-chemical differentiation. The properties of protoplasm are dependent as much upon the particular pattern of spatial relationships existing between the elements as upon the nature of these elements. Chemical analysis tends in many instances to destroy this pattern. The analyst loses sight of the very togetherness and wholeness which he would understand, for the inference to be drawn from his procedure is that he is dealing with structureless mixtures of elements.

Changes in function

Numerous biologists, as for instance Kassowitz and Conklin, have developed theories of aging based upon a declining metabolic rate. We have been unable to find, however, that these theories have been supported by any substantial direct experimentation. Benedict has emphasized a decrease in the permeability of the cell membrane with senility in plants, and Osterhout has associated loss of permeability with diminishing conductivity. Child estimated metabolism indirectly by measuring the susceptibility of the organism to cyanides. To prove the relationship of susceptibility and metabolic rate he states that "susceptibility is altered by motor activity, that the temperature coefficient of susceptibility is of the same order of magnitude as that of most chemical reactions and that differences in carbon-dioxide production correspond to differences in susceptibility." From Child's long series of experiments it is evident that susceptibility decreases with age, and from the work of other investigators it appears that the metabolic rate per unit mass declines likewise, but that the former is dependent upon the latter has not been shown. Even if two functions are compared at infrequent intervals and seem to be changing in the same direction, it can hardly be assumed, unless their rates of change are parallel, that they are directly interdependent. Measuring one will not be more than a rough index of the other. It seems that, although the two are in some way related, the evidence is not conclusive that susceptibility to cyanides and anesthetics runs parallel to metabolism. Herlant's experiments, for instance, with the effect of various kinds of poison on eggs suggest by analogy that the times of maximum susceptibility to water soluble and fat soluble toxins respectively are not synchronous in ontogeny. Tests for susceptibility are furthermore not very precise, and the CO_2 output alone, without O_2 determination, is not an entirely satisfactory criterion of

metabolic rate, particularly under abnormal conditions.

Whatever may be the basis of susceptibility, it is a phenomenon of great biological importance, and Child's experiments are of considerable pertinence. Concentrations of the injurious substances were used which kill the organisms within a few hours. There were morphological criteria for the degree of "aliveness" by which at intervals after administration the observer could estimate the effect of the poison. Adaptability or, as Child calls it, acclimation was tested by using concentrations of narcotics which were insufficient to kill within a short period. Organisms for a time seemed to become adapted to such a medium. Death came later, after one or more days. The results of these investigations indicated that the younger tissues were the more susceptible as well as the more adaptable. That is to say, with strong doses they died more rapidly, but with the doses to which acclimation was possible they outlived cells of greater physiological age. Child was not concerned with the rate at which functions, such as stability and mobility, changed with life. Other experiments, conceived as were Child's, have been reported. Tumor cells are generally considered to have the characteristics of young tissue, and their hyper-susceptibility to x-rays and other agents is well known. Warburg, Posener, and Negelein have shown that a similarity exists between the tissues of embryos and of tumor cells in the relation of respiration to glycolysis. The rapidly growing embryos can and do exhibit the phenomenon of aerobic glycolysis to a slight extent, though relying on this function in comparison with rat carcinoma only in the ratio of about 1 to 40. Cramer has shown that susceptibility to x-rays is directly correlated with water content, which in turn is a function of age. Riddle showed that age was the most important factor in determining the death or survival of embryos subjected to abnormal oxygen tensions.

Susceptibility of a different nature, that for instance which is concerned with the reaction to tumor implants, was shown by Murphy to decrease with age in the chicken embryo, or more exactly, resistance to tumor growth seemed to be entirely absent until the 18th day of incubation. At this time small transplants of rat sarcoma would no longer "take," and, even if in full growth at the time, thenceforth became encapsulated and began to show signs of degenerative change.

Brody and his collaborators have used various criteria such as milk secretion and egg production for estimating the rate of aging. It was found here as with growth that an equation of the monomolecular form would describe the relation between age and the empirically ascertained quantities, thus supporting Robertson's theory of the kinetics of senescence. When the growth period is included in the curve describing functional activity, the entire span may be described "by an equation containing two exponential terms which is practically the equation used to represent the course of accumulation and disappearance of a substance as the result of two simultaneous consecutive monomolecular chemical reactions" (Brody). Needham has concerned himself with an analytical study of metabolism. He has reviewed in a comprehensive fashion the metabolism of the developing egg; and further has shown that during the embryological period of the chick there is a succession of energy sources in the order, carbohydrate, protein, and fat.

There is need for a thorough investigation of metabolism in terms of age in some of the lower forms of life for correlation

with successive chemical analyses of the tissues. Life may be viewed in the simplest quantitative terms as exchanges of energy between the organism and its environment, and as transformations, that is to say redistribution, synthesis, storage, and oxidation, of the assimilated energy within the body. Katabolism is the *sine qua non* of life, the heat evolved, as with a coal fire, providing the necessary conditions for its own continued activity. Under basal conditions approximately the minimal heat for the maintenance of life is provided by chemical action. This is the justification for saying that the organism burns in its own flame.

Duration of life

Any discussion of senescence must include a consideration of the factors which affect the velocity of the process. In this connection Loeb and Northrop have made conclusive experiments to show the influence of temperature upon the duration of life of a poikilothermal animal. They found that the life span of sterile flies maintained at different temperatures was considerably shortened by the application of heat; and that the temperature coefficient obtained for these observations was such as one finds for chemical reactions. It seemed, therefore, that life might be viewed as if it were a chemical reaction, which ceased as soon as there was depletion of a particular "life substance" or the accumulation of inhibiting end-products had reached a certain level. The metabolic rate might be accelerated by motor activity as well as by external temperature. Slonaker's few experiments, in which the duration of life in rats forced to exercise in a revolving cage was compared with that of rats kept in stationary cages, showed that under the conditions of the experiment a large amount of exercise was detrimental to longevity.

Other factors having a bearing on this problem have also been studied. Pearl has lately reviewed and summarized the work of eugenicists and statisticians relating the influence of heredity to the length of life. The most reliable and comprehensive data appear to indicate that the dominating factor conditioning the duration of life in a constant environment is an inherited one. Pearl's experiments with *Drosophila* show, furthermore, that the inheritance in question conforms to Mendelian standards. Pearl summarized his general viewpoint by suggesting that heredity probably acts by determining "within fairly narrow limits, the total energy output which the individual can exhibit in its life time," and that the "manner in which the environmental forces chiefly act in determining duration of life, appears to be by changing the rate of metabolism of the individual."

PHYSIOLOGY

Normal and pathological

The process of becoming can be illustrated also in more complex organisms and indeed in the physiology of man and in the changing susceptibility to disease which he manifests. It is perhaps unnecessary to refer to changes in structure which take place with advancing years. They are on the whole general knowledge and can easily be recognized. We refer here of course to the gradual changes in hair, eyes, and skin, to the alterations in the solid viscera and in the blood vessels; to the involution of the skeleton and of the muscles. It is not these so much as the changes which take place in function to which we desire to direct attention.

As an expression of the general activity of an organism the basal metabolism may be selected. We venture the opinion, in which Du Bois apparently concurs, that at all ages, but especially at the more ad-

vanced ones, more data are required before a definitive curve of change with time can be regarded as established. It is not only that more data are wanted; the conditions under which the observations are made need more precise definition. That there is a change in the course of life is clear from the results so far published. Benedict and Talbot, as quoted by Du Bois, calculate the basal metabolism in infants to be 26.7 calories per hour per square meter of body surface. In boys aged 6 to 7 years the rate is considerably higher, 57.5, according to Magnus-Levy. At 12 to 13 years it falls to 49.9; between 20 and 50 years it falls still lower to 39.7; between 50 and 60 years it is 35.2; and, finally, between 70 and 80 years, 30 (Magnus-Levy). The curve, it appears, begins at a low level, mounts rapidly, and attains its peak at about the age of 6 years; for 30 years it remains stationary and declines slightly and gradually thereafter. Here is distinct evidence that in the course of life fundamental changes take place. Precisely what changes is not yet known; undoubtedly they are significant but whether of the development of the muscular system in the early years of life as Krogh thinks, or of the activity of a specific growth stimulus resulting from the ununiform development of the glands of internal secretion is undecided. That it is possible to draw precise curves descriptive of change with age in the basal metabolism has been shown by Murray in the case of chicken embryos.

Curves of change in other general functions have likewise been drawn. Among these the blood pressure may be reckoned, representing as it does, not the result of a simple mechanism but a resultant obviously of a number of factors. Faber and James have made measurements in children from 4 to 16 years of age. In the curve for systolic pressure they assign 89 mm. Hg. as characteristic at the age of 4 years; 100 mm. Hg., at 8 years; and from here describe a more gradual rise to 115 mm. Hg. at 16 years. The diastolic pressure undergoes similar changes during this period, rising from 60 mm. Hg. to 67 mm. Hg. between 4 and 8 years and then more rapidly to 76 mm. Hg. at 16 years. From 16 years onward data are supplied by Alvarez. The curves which he has published represent probably the best standards now available, since they are free of the fault of selection inherent in those which have been commonly used and which issue from the examination of selected groups of individuals, such as applicants for life insurance. Although Alvarez's curves are based solely on figures obtained from university students they are representative of individuals in all states of health. For men at 16 years, Alvarez gives the systolic pressure as 127 mm. Hg., considerably higher than the figure of Faber and James; from this point to 30 years, the curve falls to 118 mm. Hg. In the case of women it begins at 118 mm. Hg. at 16 years and falls to 111 mm. Hg. at 24 years. After this, the curve again rises in the case of both sexes. If the curves described by Alvarez are correct—and they have to recommend them great care in the collection of the data—a new factor in the movement of the blood pressure with time emerges, namely, the fall in the curve between the ages of 16 and 24 years. The meaning of this change is still obscure and obviously requires further investigation for its clarification. For females, results similar to those of Alvarez have been published by Burlage. His figure, 104 mm. Hg. at 9 years, may be compared with that of Faber and James (101 mm. Hg.); at 14 years he gives 124 mm. Hg.; at 18 years, 114 mm. Hg. The last figure is to be compared with that given by Alvarez (118 mm. Hg. at 16 years) and

with Faber and James's (115 mm. Hg. at 16 years); at 26 years he gives 110 mm. Hg., to be compared with that assigned by Alvarez (111 mm. Hg. at 24 years).

Among the more general functions may also be placed immune reactions. Information on the relation of age to these is unfortunately not precise. But it is known in a general way that susceptibility to infection by several disease-producing agents is linked to age. Less importance must be placed on the fact that to certain of these diseases children are susceptible rather than adults who have attained the immune state than on the fact that children become infected by these illnesses at rather definite ages. Young children, for instance, are rarely infected by typhoid fever; and when it occurs in them, its course is mild. A similar statement may be made in the case of lobar pneumonia; and here again, the severity of the disease tends to be light. Young children are prone, however, to diseases of the exanthematous type. And again the incidence of rheumatic fever appears to be highest at 5 to 7 years (Ingerman and Wilson). It is a striking fact that children suffering from mumps are not troubled with orchitis as a complication until spermatogenesis has been established. (We are indebted to Dr. T. M. Rivers for this statement and for certain of the references which follow.)

Comparable information connected with immune reactions may be drawn from experiments on related matters in animals. It is stated that the skin of older guinea pigs is more sensitive to the action of diphtheria toxin than the skin of younger animals (Coca, Russell, and Baughman). The skin of the younger animals is likewise little if at all sensitive to watery extracts of tubercle bacilli; even though the regional lymph nodes and the spleen show evidence of the presence of the disease (Freund), while the skin of older ones readily shows this phenomenon. The nuclear inclusion bodies found in the testicles of certain monkeys, when inoculated with varicella virus, can be demonstrated only in young animals before spermatogenesis has been established, the reverse of the situation in the orchitis of mumps.

Of other more general functions such as that having to do with repair, little is accurately known in the case of man. Du Nouy has published information on differences in the rate of wound healing showing that this decreases with increase in age. In animals on the other hand more precise observations have been made. In rats, for instance, Mackay, Mackay, and Addis have found that after one kidney has been removed the other undergoes hypertrophy and does so the more, the younger the animal. At one month of age, the per cent of hypertrophy is given by them as 52.6; at 3 months, 36.7; at 6 months, 32.8 and at 12 months, 32.2. That compensatory hypertrophy of the remaining kidney takes place was found also by Arataki. His experiments unfortunately do not contribute to the relation of repair to age. The rats he studied were all young, the groups being 20 days and 50 days old. On the basis of a life span of 500 days, these ages correspond to 3 and 7½ years in man; that is to say to ages at which sharp differences in behavior may not be expected to occur.

Several mechanisms of a more detailed nature than those to which reference has so far been made and in which a relation to the age of the organism has been shown to exist have been described. Gilbert recorded very simple but important observations on the change in effect which he noticed on the rate of the heart, when he pressed the vagus (the inhibitory) nerves in man. He found that with in-

creasing age the effect of this maneuver increases, that is to say, the rate of the heart decreases; and in a similar manner, that the interval between the time of contraction of the auricles and that of the ventricles lengthens out. Crawford studied a related phenomenon by observing the changing rate of increase of the heart following the injection of atropine. He found that the increase is maximal at 20 to 30 years, but that after this period the rate declines, at first slowly, but after 50 years quite sharply. In respect to both functions, then, time plays a rôle.

Studies of the vascular system have yielded data that illuminate the point that we are emphasizing. It has been found that change takes place in the degree of elasticity in human arteries. This change has been measured in terms of the velocity of the pulse wave and consists in a rise during life. Friberger found that in normal persons the rate between 16 and 25 years is 7.9 meters per second; and between 26 and 33 years, 9.2 meters per second. In persons in whom the arteries are thickened, the figure is a little higher, being 8.2 meters per second between 16 and 25 years; 9.4 between 26 and 33 years; the same between 45 and 55 years; and 10.1 over 55 years. Bramwell pursued this phase of the matter further with a more accurate technique. He found that a smooth curve might be drawn expressive of the experimental data. According to his curve the mean velocity is placed at 5.2 meters per second at 5 years; 6.2 at 20 years; 7.2 at 40 years; 8.0 at 60 years; and 8.55 at 80 years. These results are lower than Friberger's. But the point of interest is not the absolute figure but the fact that curves can be drawn illustrative of the general view we are maintaining that functions change with time. Daly has recently published data on a related subject, in this instance dealing with dogs. He found the "potential capacity increment," by which he means the extra amount of blood that the arterial system can take up, is large in young animals as compared with old ones.

When the blood itself is examined a number of interesting facts come to light. To begin with, the white cells change conspicuously in number, as Addison and Richter show. At birth they number between 17,000 and 18,000 per cc; a week later they fall to 15,000, and in adults they fall still further to between 5,000 and 10,000. In albino rats the course of events is strikingly different. Here, instead of falling, they rise with time. On the 18th fetal day, they number about 1,000; there are 2,000 at birth, 5,000 on the 5th day, and 8,000 at maturity. The red blood cells also change, decreasing in man from seven or eight million at birth to four or five million at maturity. In albino rats the change is again in the opposite direction, for in them on the 18th fetal day there are two million red cells, three million at birth, and seven to nine million at maturity.

Aside from formed elements other constituents of the blood, notably hemoglobin, undergo quantitative change. Whipple has shown in dogs that at 1 month the content is 50 mgm. per 100 cc, and at 1 to 5 years, 120 mgm. Between 10 and 12 years there is a slight fall to 110 mgm. The changes in muscle hemoglobin are much more striking. Heart muscle, for instance, contains 100 to 200 mgm. per 100 grams in the first few months; at 8 to 9 months, 300 mgm.; and between 300 and 400 mgm. when the animals reach adult life. Unfortunately neither the water content nor the total dry substance is given.

An interesting report is that of Bürger and Schlomka. (This publication came to our notice after the preparation of this

report was complete.) Like us they are interested in distinguishing normal from pathological processes in the course of aging. They selected for study especially tissues in which the rate of metabolism is slow and, as typical of this group, the cartilage of human ribs. This tissue loses water to the fourth decade; nitrogen apparently increases, in consequence, for its relation to dry substance remains constant. Cholesterin, however, actually increases; and so does calcium. These changes, as well as those seen in the cornea and in the walls of blood vessels, are the physiological result of aging and are not to be regarded as abnormal processes.

Differences have been described also in the chemical constituents of the blood. Tisdale and Harris, for instance, have found that at about 16 years phosphorus falls from 5.4 mgm. per 100 cc. serum to 3.8 mgm. Should rickets occur in early years the phosphorus level may fall to 3.0 mgm.; and conversely, in case of the fracture of bones in adult life, its amount rises toward the early high figure of 5.4 mgm.

Age also influences the amount and behavior of sugar in the blood. The basal amount averages according to Punschel 0.094 per cent between 16 and 34 years, 0.106 per cent between 58 and 70 years, and 0.110 per cent over 70 years. If 20 gms. of sugar are given by mouth, the quantities in the blood rise to 0.137 per cent, 0.153 per cent, and 0.163 per cent respectively at these ages; that is to say, the rise is greater the greater the age. Hyperglycemia follows ingestion. The period during which this state can be demonstrated to persist also varies with age. The figures are found to be 76 minutes, 99 minutes and 109 minutes; if 76 minutes is made to equal 100 per cent, 99 minutes equals 131 per cent and 109 minutes, 144 per cent. Hale-White and Payne found different figures but likewise concluded that the content of sugar in the blood varied with age, that its level was the higher the greater the age, and that the older the subject the longer did hyperglycemia persist after its ingestion.

In chickens, Baker and Carrel have found a relation to age in the content of lecithin and lipoid in the blood. The concentration of these substances increases, but cholesterol decreases with age. Hanes has shown likewise in chickens that the character of fat in the liver changes conspicuously during the embryonic period. During the first two weeks there are for the most part lipoids in which phosphorized fats predominate. These are isotropic. Later the character of the fat changes. There are instead esters of cholesterol, which are anisotropic. This metamorphosis is apparently associated with the process of calcification taking place elsewhere in the organism in the course of which phosphorized fats supply phosphoric acid. In rats, Falk, Noyes, and Sugiura describe progressive changes varying from 3 days before birth to 3 years 15 days. They measured concentration in terms of the ester hydrolyzing and lipase actions exerted by extracts of whole rats. The action increases from 2 days before birth to 126 days; finally in old rats at 1110 days there is a return to the behavior noticed at 27 days.

This bare catalogue of facts has an interest apart from its mere recital. The collection of such facts and others of a like nature should provide a basis for arriving at a more satisfactory notion of the mechanism underlying the aging process. To the readily recognized changes in morphology, especially in man, of which daily experience makes one easily aware, attention need not, as we have pointed out, be directed. Nor is it necessary to do so in the case of such

physiological phenomena as are representative of the sexual life, especially in women, nor to the change from feebleness to vigor in the young and again from vigor to feebleness in old age. But of the changes either in structure or in function which lie behind these manifestations there can scarcely be said to be more than a beginning of exact analysis. It is mechanisms of this nature which the present series of investigations is designed to analyse. The publications called Physiological Ontogeny (Jour. Gen. Physiol., 1925–26. ix. 1–37, 39–48, 405–432, 603–619, 621–624, 781–788, 789–803; 1926–27. x. 337–343. Jour. Exper. Med., 1925. xlii. 275–290, 291–297, 299–310), some of which have already been published and to which this essay serves as an introduction, illustrate the viewpoint from which this investigation is being pursued. It is not difficult to see what are the sources of our interest in this matter. The facts of course have an interest on their own account, apart from the satisfaction that comes from bringing a greater measure of order into what appear to be unrelated phenomena. The more exactly they are collected and the more extensively they are correlated with other phenomena, the more clearly will emerge the conception that the study of physiology must consider mechanisms not only as they appear at a fixed period in the life history of an organism but must extend its view to embrace in its descriptions the changes which take place from birth to death. For an analysis of a function which is correct and complete during adolescence need no longer be, and indeed often is not, descriptive either of maturity or of senescence. In this view physiology will become the description, not of a point, but of a curve. It will be a matter of singular advantage to possess curves of normal form and of normal behavior coextensive with the span of life. These will facilitate judgment of what are average manifestations of life, year by year and decade by decade. In the domain of medicine we shall be classifying quite differently phenomena which now pass as evidences of disease. Many of them we shall be recognizing as appearances characteristic of the senescent or of some other normal state. How far reaching a change in orientation may take place in the practical world of medicine in consequence of a realization of the meaning of new definitions, it is not possible to do more than to suggest. But one can foresee that there reside implications in this outlook which are significant for the future of research and for the application of therapeutics. In point of fact study in the process and state of senescence will suggest directions for research distinctly different from those devoted solely to the hope of preventing or of curing its manifestations.

THEORETICAL CONSIDERATIONS

We have reviewed what we believe to be the chief facts relevant to the problem of ontogeny in the domains of general and human biology, normal and abnormal. On the basis of these and other findings men have speculated about the "causes" of aging and have developed concepts to "explain" senescence and death. Various theories have been proposed engendering differences of opinion, some of which seem to have been due to a disregard of the fact that all hypotheses do not belong in the same category and for this reason may not be compared. Another cause of confusion is a prevalent belief that one factor to the exclusion of all others must be found to account for the phenomena.

It does not seem to be universally evident that the same phenomenon may be viewed in a number of distinct and mutually independent aspects. It is often

assumed that the most dispassionate quantitative description of nature is that made possible by statistical methods, a subject that we shall discuss later. But scientists, who in the end are human, have always interested themselves in causes; so that even now, despite Hume's logic, they proceed in their experimentation as if the doctrine of causation were a rational induction from experimental knowledge. Causal biological theories have fallen naturally into two categories, the mechanistic and the functional or teleological. The *mechanistic*, which entail the proverbial infinite regress, rest finally upon such convenient subjective concepts as force, energy, and affinity, whereas the *teleological* theories are directed towards the future, towards either (1) an ideal, living, perhaps anthropocentric goal, as in the case of the "survival of the fit" concept, or (2) a mathematical, esthetic, fixed termination, such as the "least action" law. These are so-called final causes.

From the standpoint of *efficient causation* the problem of ontogeny is exceedingly difficult. Many processes related mysteriously one with another are all occurring simultaneously. Which are the significant ones? One thing is now certain, that no clear understanding of the concrete fact of evolution can be reached from a one-sided approach.

Hitherto there seems to have been an undue insistence upon describing the life process in terms of some one variable, whereas it is possible that ground may exist for harmony between many of the theories recently in dispute. For instance, with the literature in mind, it may be said that life is characterized by an *attractive or integrating force* (Spencer), exemplified in the molecular sphere by an increase in the size and complexity of the protoplasmic units (Müller, Cohnheim, Bühler, Rubner) or more generally by a change in the "physico-chemical substratum of the cell" (Child). This leads to a concentration of solids (non-electrolytes), so that permeability (Benedict) and electrical conductivity (Osterhout) become diminished. As a result the velocity of chemical change is lessened, and consequently the nucleus, which is believed to be the regulator or organizing centre of cellular metabolism (Conklin), shows a special and relatively greater integration, as for instance in the decrease in the nucleoprotoplasmic ratio. Excretion becomes progressively less efficient, and the end-products of metabolism accumulate in the cell (Jickeli, Montgomery). In the cytoplasm, owing to the gradual cessation of motion with the accumulation and concentration of matter (Liebermann), precipitations or agglutinations of matter occur, giving rise to metaplastic granules (Mühlmann, Kassowitz). These still further limit metabolism and accelerate a vicious cycle.

In such a way it may be possible to weave together in a general, but to be sure rather vague, way the principal "causes" proposed as "explanations" of aging. Naturally, for certain purposes it is permissible to regard evolution in such terms as membrane permeability, colloidal flocculation, or nucleo-plasmic ratio, but these are necessarily one-sided views and inadequately descriptive. Since there is reason to believe that a knowledge of the successive *physico-chemical* states of the proteins in protoplasm would give us the best description of the fundamental changes with age in living tissue, frequent analogies to the aging of colloids are found in the literature. For instance some solutions, such as silicic acid, when freshly prepared are easily dialyzable but lose this power on standing. Small particles aggregate into larger units, which flocculate more easily or do so spontaneously. When unstirred, colloids

become more stable. Bechhold says that gels become less elastic and optically less homogeneous or turbid, and that a high temperature accelerates these changes. These are characteristics shared by aging tissue. Possibly division and reproduction of cells correspond to the preparation of a fresh colloidal suspension but, as with age cells divide with diminishing frequency, this freshening process is less frequent and, perhaps owing to the changing milieu, less complete.

As certain glands of the body have special functions in regulating growth, as for example the thyroid, thymus, pituitary, and gonads, and as the tissues of these parts must also undergo the above mentioned orderly modifications in constitution and behavior, their secretions must likewise change quantitatively with time. The discovery of growth or metabolism modifying principles in the blood serum or tissue juices, though of great interest, does not in any way change the nature of the problem. For since these activators and inactivators are themselves products of tissue dynamics, we are driven back to an investigation of the latter to account for the age changes in the concentration of the former. But the existence of this fact does not make futile, or any the less interesting, the search for special agents, for a part of the problem of mechanistic causation involves a search for these specially differentiated processes or areas that have dominance in regulating the velocity and nature of other vital activity throughout the body. As a result of considerations like these comes up the question of the leaders of the ontogenetic process—whether considered anatomically, cytologically, or chemically. Experimental embryologists have within recent years, following the guiding experiments of Spemann, shown that there is a hierarchial regional control in the body, that certain parts of inherent high potential control, even when transplanted to foreign parts, the activity and development of the cells around them. For instance embryonal skin cells of the abdominal wall are made to develop into a normal lens under the influence of optic cusp tissue transplanted into their midst. Jones calls this mysterious organizing principle, cytoclesis. Regions of dominance are seen to determine the activity about them and modify both the quantity and the quality of differentiation. There are innumerable instances also where one part inhibits the immediately adjacent parts, where one zone becomes suddenly marked out for growth and its surroundings are repressed in their activity. This fits in very well with Child's work in which he showed that in worms, dominance was associated with high metabolic rate, and that in some of the lower forms he could distinguish so-called metabolic gradients, forming an axis, the structural characteristics and physiological phenomena being also related to this axis. Lillie believes that these apical active regions are negative to the basal, less active parts. Bioelectric currents are in consequence set up which may have an influence on neighboring parts even when there is no tissue continuity between them. On this plan we find a metabolic hierarchy in the microcosm, the mainspring being the point of high oxidation or the independent variable in the developmental process.

To other investigators similar ideas on the order of phenomena have appeared to be relevant in the domain of chemical activity. For in successive chemical reactions and in the accompanying redistribution of elements, some substances apparently have greater mobility, greater permeability, and a greater migratory rate than others. Viewed from these

several angles the idea seems to gain force that one constituent takes the lead in the evolutionary process, whereas the others show relative degrees of lag.

If, when a complex equilibrium is disturbed, one of the elements is found to move with the greatest velocity to reach in the shortest time a second relatively fixed state, it does not signify that that element is the "cause" of the chemical reaction. For instance, because CO_2 diffuses faster than O_2 through the pulmonary epithelium, need it be considered more than a link in the respiratory gas cycle? And again, because in the electrolysis of sodium chloride the migratory rate of $Cl-$ ions is greater than that of $Na+$ ions, are we thereby to understand that the electrical phenomenon is "caused" by the chloride ions? Such considerations are relevant to the evolutionary differentiation of protoplasm, in the course of which some constituents reach steady states before others, and so the phenomenon of molecular change in the presence of a more or less constant milieu is found.

But in any case it is clear that the ontogenetic process is no simple affair, no matter which chemical leadership or master-reaction develops during any one period, nor should one expect any determining leadership to last. The sudden emergence of a mutant reaction or novelty should be expected as a frequent occurrence during ontogeny. We are prepared to find that new substances and new forms spring or are forced into being when the milieu provides the necessary and adequate conditions.

One of the most satisfying theories to account for organic aging was, it seems, first proposed by Spencer, and later widely discussed and accepted by others. It called attention to the changing relationship between surface and volume as the necessary concomitant of growth. It is in the very nature of geometric relations that with growth the volume or mass increases as the cube, and the surface as the square of a number. The result from a biological standpoint is that for a unit mass of active protoplasm undergoing continuous chemical changes, the portals, that is to say, the surfaces of the organism for entry and exit of the substances which are the antecedents or products of vital activity become continuously smaller, and therefore continuously less suitable for maintaining the original velocity of metabolism. There must necessarily follow a diminution of activity and all the other changes that are merely the logical outcome of the initial modification. This may prove to be the crux of the problem, all the important surface areas of the body, skin, gastro-intestinal, renal, pulmonary, cellular, and molecular, being nicely, mutually balanced to one another, and organically adjusted to the metabolic rate. This argument depends on the analogy which has been chosen, namely, the properties of the sphere. There is presumably nothing to prevent the surface of an organism from attaining any area regardless of its mass, by the development of infoldings for instance, unless it be the principle of efficiency which would dictate an approximation to the spherical state. A relatively large surface is a great expense.

There is, however, another approach to this problem, apart from mechanistic theories; the successive stages of an individual life cycle may be examined and described in *teleological* terms. Instead of attempting to "explain" the changes with age in terms of established physicochemical laws, one can enquire: What purpose do they fulfill? What part do they play in maintaining in the organization the stability and thus the integrity

of the individual? In what way do given changes increase survival value? This viewpoint is in no manner contrary to mechanistic concepts, but may be used as corollary to them. For instance, Weismann's notion, to the support of which Pike has recently come, that individual death is an inherited characteristic that has become fixed by natural selection, is a teleological theory, arising from considerations of racial interest. Pearl, evidently believing that the acceptance of this view would tend to destroy the validity of mechanistic principles, has said that "probably no more perverse extension of the theory of natural selection than this was ever made." But Pearl himself believes that death is the result of differentiation, that "natural death, as distinguished from accidental death, is preceded by definite structural and functional changes in the body." It follows that death is the final senescent state. Senescence is in short a process innate and inherent in the life of protoplasm. Then since, as Pearl himself seems to admit, senescence (that is to say natural death) and somatic differentiation are positively correlated, never independent, and hence for the purpose of this argument synonymous, Weismann's statement amounts to little more than to saying that somatic differentiation has survival value for the race. The soma itself, since it cannot give rise to new individuals, must perish. Life after reproductive functional atrophy has become established represents the reserve capacity or margin of safety for continued existence which is commonly found in nature. In imagination we may reconstruct a picture in which at the moment of emergence of metazoan from protozoan life competition between the wholly immortal protozoa and the partly immortal metazoa took place.

The metazoa have survived the struggle; their plan of organization provides for soma and germ plasm. For germ plasm there is unbroken descent down the ages, but for the soma, individually and elaborately differentiated though it is, there is only a series of successive deaths. Procreation is the crucial function; the soma is in this sense superfluous. This seems to have been Weismann's meaning, and Pike's. There can be little doubt that the motive for the belief that the preservation of life is of paramount importance has an anthropocentric origin; that the mechanisms which are concerned in bringing about survival of the soma have intuitively become the subject of major interest. There seems to be a directive tendency in organic phenomena which lends color to man's inherent wishfulness. These he names reactions, reflexes, instincts, and pre-dispositions. Nature's goal seems to correspond to his own. Natural phenomena may, therefore, be investigated in the light of this goal as if they had a function for a telos, that is to say, for the preservation of organic existence.

There is still another group or type of explanation for the life process also to be classed with final causes. These point out that there is a tendency on the part of mechanisms to move toward some final condition or fixed state. These have an esthetic motive and are derivations of or analogous to the Second Law of thermodynamics. Aristotle was not far from the general idea of degradation when he spoke of the innate heat existing at birth and of its gradual dissipation during life, a phenomenon which was responsible for senescence and death. Thermodynamic reasoning applied to ontogeny yields approximately the same result; the terms according to which the argument proceeds make little difference, whether it is of change from instability to stability or from

the homogeneous to the heterogeneous, or whether the appeal is to the concept of organization or to the principle of least action. In all, increase in entropy, or death, is the final state. But if the universe were governed solely by this principle, why, since time is infinite, is there, as Boltzman has asked, any free energy left in the universe? And the answer must be that there is another principle of an opposite and compensating character, a principle still hidden, which from its nature may be forever hidden from scientific investigation. Chvolson's statement that "the second law is the law of evolution of the world accessible to our observation," is in accord with the facts of ontogeny as we know them. The natural history of an organism from birth to death is the change from greater to less chemical activity per unit mass compatible with life. In the case of the ameba there is a periodic phase of reversibility associated with division, in which there is a complete return to the initial condition of high polarity and metabolism. From this point of view sexual and asexual reproduction are essentially the same. The act of creation synthesizes the lost energy. It is as if fertilization explosively and mysteriously lifted a pendulum to its highest summit and the rest of life were the story of the gradual decrease in the amplitude of its swings. In this sense the law of the degradation of energy describes the life process itself; it satisfies mathematical, esthetic, and sensational predispositions. Other descriptions would arise satisfying to psychological, emotional, and action values. The action would be interpreted in terms of reaction. The gradual fall of the pendulum would represent a direction towards the succeeding lift. The ameba hurrying through his life cycle would be ever approaching childhood, that is to say, redivision. We do not escape from our fundamental motives; these two human tendencies creep into scientific outlooks. In the ameba, the mortality of the individual as an integral unit is contrasted in most striking terms with the immortality of the germplasm. Has science any explanation for the rejuvenescence occurring with fertilization? How is the initial energy restored to the daughter cells? On the inability of science to cope with such questions vitalists have thrived.

In reviewing the hypotheses and generalizations of later biologists one is impressed by the fact that since the days of Herbert Spencer very few important biological conceptions have been contributed to modify his system. Evolution, of which ontogeny is a particular example, in his view "was an integration of matter and concomitant dissipation of motion, during which the matter passes from indefinite, incoherent homogeneity to a definite, coherent heterogeneity; and during which the retained motion undergoes a parallel transformation." This statement has close suitability to the statements of later observers, namely, that development is characterized by an increase in size or growth, a decrease in chemical activity or metabolism, a differentiation and specialization of form and function, and a more efficient organization resulting in greater internal uniformity and stability.

Since Spencer's original formulations the most significant contributions germane to our problem have been:

(1) The distinction between cells organized into an individual whole (a multicellular organism) and unorganized cells, that is to say cells with no collective function, as in the case of unicellular organisms, tissue cultures in vitro, and tumor cells. For these advances Galton,

Weismann, Woodruff, Jennings, Harrison, Carrel, Leo Loeb, and others are chiefly responsible.

(2) Experiments showing the nature and significance of dedifferentiation and rejuvenescence in the life cycle (Child).

(3) The factors influencing the duration of life (a) inherited and (b) environmental, elucidated by the work of Bell, Pearson, Pearl, and Jacques Loeb.

(4) The concept of emergent evolution (Lloyd Morgan) and

(5) The principle of organization and the concept of organism as developed by Henderson and Whitehead respectively.

The most comprehensive recent generalizations to describe development and senescence have been made by Child. He states that "senescence is primarily a decrease in rate of dynamic processes conditioned by the accumulation, differentiation, and other associated changes, of the material of the colloid substratum." This statement is very similar to, but somewhat less descriptive and comprehensive than Spencer's dictum.

There is still another, and in this summary, final approach to our problem, independent of all preliminary intuitions about efficient and final causes, and that is the method of quantitative description by statistical analysis. Death is the end-point of an aging process of the greatest possible complexity, which starts at birth. From what was said in the discussion of efficient causes it is clear that aging cannot be described in terms of one function. The most adequate account, as Müller predicted long ago, is the measurement of co-existences. The methods devised by Galton and elaborated by his followers make it possible to carry on this method in a systematic quantitative fashion. The nomographic method applied so successfully by Henderson to the study of the blood stands as a successful typical example for physiological description. For ontogeny the greater complexities of the living organism and the introduction of another dimension, Time, increase the difficulty of the problem. The omission of significant factors makes the description inadequate, the inclusion of irrelevant matter makes it cumbersome. This method, though tedious, seems to offer the best prospects of unearthing the more significant correlations and hence of discovering the fundamental physico-chemical changes, which would presumably provide a basis for a better understanding of the evolutionary process. Pure description has often been the necessary preliminary to "explanation" or has often by itself been regarded as the "explanation."

EXPERIMENTAL CONSIDERATIONS

Reflection upon the facts and theories reviewed, however briefly, in this paper, leads naturally to a belief in the importance of a comprehensive investigation of the same organism simultaneously undertaken from a number of distinct standpoints over the entire ontogenetic period or at least over a certain specified portion of the life span. A study so planned seems especially significant when the present day trend of biological interest towards an examination of the togetherness or totality of the organism is appreciated.

This statement applies no more to the whole organism than to any one of its parts, the heart for instance, which may specially concern the investigator. Heart muscle, as a representative tissue, is especially suitable for a number of important physiological, chemical, and physical measurements. A study of its energetics in relation to senescence seems, moreover, to be the first logical step in the further elucidation of the problem of chronic heart disease.

The extent of the duration of life of

many living forms necessitates at least a preliminary concentration upon some one period of the cycle. Usually there are three periods, embryonic, infantile, and adolescent, which are characterized by accelerated evolution and which for this reason offer the most appropriate conditions for systematic observation. Of these three periods the embryonic is by far the most important, both because during this time the changes are many times more pronounced and easily measurable, and because of the phylogenetic references.

Long ago it became evident that the Biogenetic Law, which states that ontogeny follows phylogeny, was untenable, for it was noted that each new development or emergence could not be forecast from the very beginning and that each ontogeny showed variance in every stage. The two series, phylogeny and ontogeny, stand nevertheless as crudely analogous phenomena, and, lacking a complete paleontological record for any one species, ontogeny may be taken to present the best record that we possess of racial trend.

Tangl has pointed out that the water content of the organism decreases with development both in phylogeny and ontogeny; and it appears that such is also true for the calorific value per unit mass of tissue. Does the sudden desiccation of the tissues during the growth of the embryo correspond to the emergence from aquatic life? This and other questions of a like nature present themselves and emphasize the peculiar importance of the embryonic period.

The difficulty of physiological experiments upon mammalian embryos led us to choose the egg, or more specifically the chicken embryo, as the object for study. A number of other unforeseen advantages presented themselves, among which may be mentioned the fact that (1) the environment, consisting of the surrounding atmosphere and the food supply of the embryo, that is to say the yolk and albumen, is relatively stable, (2) the age of the organism may be closely estimated, (3) the initial poikilothermal and eventual homoiothermal nature of the chick allows for an investigation of temperature effects and of the development of a mechanism for internal control, (4) the embryos are sterile, a fact which enhanced the facility with which various operations, such as tissue cultivation, could be performed, (5) the supply of fertile eggs from hens of the same breed was plentiful and sufficient at all times for our needs, and (6) the chicken embryo has always played a leading rôle among the objects of biological investigation. Aristotle, Fabricius, Harvey, Malpighi, John Hunter, and Haller, it is known, made studies upon its development, Wolff used it for microscopic examination when he overturned the firmly rooted theory of preformation, and since the latter's day it has been studied by embryologists more intensively than any other species.

A knowledge of form is important to parallel the physiological studies, since the problem of the functional equivalence of structure depends upon correlations between the two. The change in character or value of each function as incubation advances and the rate and acceleration of the change will be matters of interest and phenomena for comparison. Heretofore interest has not been sufficiently directed towards the question of velocity, except when concerned with the problem of growth. It has been stated that with age changes such as dehydration and decrease in the heart rate occurred but never at what rate these took place. This conclusion has often been reached by comparing values at the two extremes of life. The advantage of knowing the

values intermediate between the extremes is that rates of change at different ages may be represented by the slopes of the line connecting the points, and thus the dependence of functions changing at similar rates in respect to age may be made evident. It will be found, as Lotka states, that the most important expression is not the quantity of any one factor at a given time, but rather the rate of change of that quantity at the time. In this connection it may be well to point out that rates of change will not be found uniform at all times for all tissues in the organism. It is in fact already well known, crudely, that tissues and organs exhibit changing relative significance with time and that this is reflected in their morphology. Equal growth may be designated symmetrical; unequal, asymmetrical development. We have already referred to this phenomenon in another connection (physicochemical activity); it seems not unlikely that it will play a part in our future studies.

This review is designed to present the facts and opinions found in the literature dealing with the aging process and is intended to indicate the rational considerations that underlie the investigations that have already appeared or are in process of publication.

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PLANT WATER RELATIONS

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INTRODUCTION

PERHAPS no subject in plant physiology has been discussed at greater length than the problem of the rise of water in trees. The literature of this subject has been increasing since the appearance of Stephen Hales's *Vegetable Staticks* in 1727. It is now enormous. Some phases of the earlier scientific discussions have filtered out into the realm of popular knowledge, and intelligent people everywhere are now at least aware of the existence of a peculiarly interesting problem in this connection. The ascent of sap constitutes a subject of perennial interest to many minds that are not specially devoted to plant physiology or even to any branch of natural science. The more fruitful contributions toward an appreciation of this very fundamental natural process are, however, of recent date, for what now seems to be the basic clue to the mechanics of the rise of water in trees did not get adequately presented until the appearance of Dixon's publication in 1909. Study in this field has gone on with renewed vigor since that time, and the general principles involved in the "transpiration stream" appear now to be fairly well worked out. But these recent results have not yet reached the intelligent public; indeed, they are only beginning to be presented in school and college text books of botany, and their implications are but vaguely envisaged by many professional workers in plant physiology. Popular science and school and college science must generally lag very much behind research, but in this case the lag is remarkably great.

The physical explanation of the rise of water in trees now leads far beyond this movement itself, to problems of the entrance of water into the plant body on the one hand, and, on the other hand, to those of water retention within the plant and of water loss. Tall trees furnish an obvious example of certain apparently somewhat uncanny phases of plant water relations, but forms of low stature generally present the same problems.

From a less philosophical point of view the subject of plant water relations is of interest to all who have to do with living plants, which implies almost everybody. I may mention agriculture as the great, fundamental human occupation and then proceed to note how important water is in crop production. As the earth is constituted, water and temperature—the water supply and the heat supply—are the main limiting conditions that demark vegetational and agricultural regions. Water conditions of crop plants are readily amenable to artificial modification. Recent advance in our knowledge of how plants need water and why some forms need more to produce a crop than others has led to great improvement in irrigation and drainage. Also, attacks of fungus and insect parasites on cultivated plants are found to be related in many cases to the moisture conditions of air and soil.

In the following pages I aim to present a

general outline of plant water relations, according to the present state of knowledge. The complexity of the subject and the intricate inter-relations of the various topics that require attention render the organization of such an outline somewhat difficult and compel more or less repetition in the interest of clearness and readability; in an essay of this sort the same elementary principles need to be considered from several different points of view. I am purposely leaving out of consideration many details that remain still to be elucidated, over which discussion among specialists is now going on. Other details that seem to be fairly well understood are omitted in order that the main features may be more clearly presented. Attention is here confined to ordinary vascular plants, with root systems in water or soil and with stems and leaves in air.

The literature references given at the end of this article are calculated to place the reader in touch with some of the most useful discussions of the various topics. The very extensive literature abounds in curious vitalistic or mystical conceptions and implications, and physical principles of great variety (both real and imaginary) have been wrongly or inadequately invoked from time to time. Such material is generally left out of the present picture; it is mainly historical now. A large number of additional references to the literature, some of which may well be fully as important as many that are actually given in my list, will be found in the papers and books that do receive mention here.

THE GERMINATION OF THE SEED

The resting embryo may be regarded as a complex mass of colloidal substances containing but little water and but little dissolved material. It is structurally divided by the cell walls into apparently distinct little regions or chambers, the cells. The cell walls themselves are ultra-microscopically porous, like gels, and contain some water, held very firmly in the pore spaces by the adhesion or attraction forces that hold water in close contact with most other substances; in a word, by imbibition. According to the nature and distribution of their non-water materials, some walls contain more water than others, but we may think of them as all in water equilibrium with one another, all being as nearly saturated as the meager supply of water in the resting seed permits. The cell contents are also colloidal gels impregnated with water of imbibition, which are in approximate water equilibrium with the walls. Water is held in the walls, protoplasm, starch grains, etc., by the complex of adhesion pressures just mentioned.

In the cell cavities osmotic attraction for water is also active to a high degree in many cases, for much of the water-dissolved material of the vacuoles is greatly hindered or practically prevented from outward diffusion by osmotic membranes that line the cells. The layer of protoplasm lining the cell is nearly or quite impermeable to the osmotically active substances of the vacuole, although, like the walls, it is relatively very permeable to water. Solutes that cannot diffuse out into the walls generally develop, therefore, considerable osmotic pressure. In the embryonic tissues, whose cells have no large vacuoles, the cell cavities are filled with the protoplasmic gel, in which a considerable water content is held, partly by imbibition and partly by osmotic attraction. When the water-attracting materials are in solution and the solution is retained by superficial layers or membranes that prevent or greatly hinder the outward movement of the solutes, the attraction is osmotic; when the

particles whose surfaces hold the water are not dissolved their attraction is imbibitional. This distinction, somewhat artificial as it may prove to be, is worth while because osmotic attraction of solute for solvent is much better understood than are the attractions that tend to hold water on surfaces of materials that are not dissolved. Both kinds of pressure are probably present in nearly dry protoplasm, but osmotic pressure is surely the important feature of water retention in vacuolated cells. Most of the study of water retention by plant tissues has been based on the supposition that it is due to osmotic phenomena, and imbibition has not received much attention.

The outer layers of cells in the seed are mainly without protoplasm or contain but little. Their cell cavities are small or filled with gas, their walls are generally so made up that they hold very little water when saturated (somewhat like blotting paper that has been impregnated with varnish and then dried), and they greatly retard evaporation of water from the seed. In some cases they are almost impervious to water movement either outward or inward, even when the seed is submerged in liquid water. Some seed coats must be broken or punctured before water can enter rapidly enough and in sufficient quantity for germination.

When a seed is brought into contact with liquid water the imbibition and osmotic attractions cause water to enter. The cell walls swell more or less, as their pores are enlarged by the entering water, and the cell contents also swell. A limit to the swelling of walls is soon reached, when the cohesion of the gel (cellulose, etc.) is just balanced by the imbibition attraction. Contents of living cells are capable of much additional water absorption, but they cannot escape through the walls; as water enters, the walls are stretched until their elasticity balances the combined osmotic and imbibitional pressures acting outward from within. The cells thus become turgid and resist compression and deformation much as does an elastic solid. A turgid cell behaves much like a sheet-rubber bag (such as a foot ball) into which water has been forced until the rubber has been somewhat stretched and pressed firmly against an outer, less extensible, enclosing wall. The ordinary foot ball or automobile tire is turgid because the high internal gas pressure stretches the thin lining, forces it against the casing, and stretches the latter till its elasticity balances the distending pressure.

While the seed swells, and throughout later stages also, chemical and resulting physical changes go on in the embryonic cells. Dissolved substances like sugar and salts get transformed in complicated ways, and new protoplasm is added to what was originally present. As imbibing and osmotic material increases in a cell, more water is drawn in from the surrounding tissue (if the resistance to water absorption is not too great) and finally from outside of the seed. The whole mass of the seed, walls and cell contents alike, tends always to reach water equilibrium throughout and also in relation to the surroundings. Water moves from places where osmotic and imbibition attraction is lower to places where it is higher. The embryonic cells consequently enlarge, their walls become increasingly stretched, and the latter would be ruptured but for the fact that the metabolic processes add wall material that continually counteracts the effect of stretching. The enlarging protoplasmic masses divide, new walls are formed across older cells, and the smaller cells thus formed repeat the process of swelling and division.

THE SEEDLING

The embryo becomes a plantlet, and the plantlet becomes a plant. Non-water material is added at an adequate rate, and this addition controls the rate of water entrance, assuming an unrestricted external supply of water. But the amount of non-water material (such as sugar, salts, cellulose, etc.) requisite for a given amount of tissue enlargement is very small compared with the amount of water required. Enlarging tissues, and active tissues generally, are mostly water, to within a few points of one hundred per cent, by either weight or volume. The source of the necessary water is at first the liquid bathing the seed, which enters through the seed periphery. But roots soon protrude and add greatly to the extent of the absorbing surface, and consequently to the rate at which water can enter the organism, if only their enlarging external surfaces are kept wet.

The material used in growth, other than water, comes at first from the accumulations in the seed. Later the supply comes largely from sugar that is formed in the leaves through photosynthesis, but salts enter with the water, though at independent rates. It is interesting to note that the products of photosynthesis are formed from water and carbon dioxide and that a certain rate of water supply is therefore required even for the production of the osmotically and imbibitionally active substances and structures that attract the entering water. Some water is chemically used up in the formation of the very machine that brings in the supply needed for enlargement. On the other hand, and from the very first, water is chemically formed in the organism at a low rate through respiration and related processes, especially in active tissues. In aerobic respiration oxygen from outside of the seedling is consumed in this way. For later phases of development much of the oxygen supply for aerobic respiration may come from the photosynthetic process in illuminated green tissues. This small internal supply of chemically produced water may in some cases be quantitatively important for the growth of young seedlings not adequately supplied with water from without.

We may now suppose that our plantlet has the ordinary outfit of roots, stem, and leaves, and that the stored material of the seed has been used up. For the sake of simplicity let us suppose that the roots are in a suitable dilute salt solution, that they are submerged in liquid water. For the type of plant we have in mind the leaves are in air, and the stem connects them with the root system. The whole organism is a mass of water held in place and in shape by a remarkably small proportion of other materials, to which the water is attracted, to which it adheres. The detailed arrangement and nature of these other materials determine the form and size of the plant at any time, also its structure and its ability to retain its water against the action of forces that tend to attract water outward or to press it out.

The outer layer of the plant is finely porous cell wall impregnated with water of imbibition, and the extent of the external exposure of liquid water thus established is determined mainly by size and frequency of the ultra-microscopic pores. Some peripheral surfaces expose their imbibition water rather freely, as in the case of most young roots and root hairs; others present almost no water to the surroundings, as in the case of the epidermis of a cactus stem or the leaf of an India rubber plant.

In the interior of the plant body innumerable water-impregnated walls surround and join the living cells. These

cells are lined with osmotic membranes that tend to hinder or prevent the outward movement of osmotically active solutes, and the water of the vacuoles is thus retained by osmotic attraction. Each cell is turgid and acts as a very elastic solid, as has been said. The walls are stretched and elastic, but not stretched to the limit of their tensile strength; there is generally some extensibility to spare, and the tissue may therefore be bent or otherwise deformed to a considerable extent without rupture. But very turgid tissues with very weak walls are really brittle, as in the case of very young shoots, the pods of prime stringless beans, etc. The protoplasmic linings of two adjacent cells are, in many cases at least, made continuous by plasmodesmi, intercellular protoplasmic plugs of microscopic diameter, which occupy corresponding microscopic openings in the intervening wall.

Besides the living cells there are other spaces or chambers within the plant body, not filled nor even lined with protoplasm, but entirely surrounded by water-impregnated walls just as are the living cells. Some of these represent dead cells. Typical vessels, which extend from root to leaf in the vascular bundles, are linear series of cells from which the original protoplasm has disappeared and in which many of the cross walls have been wholly or partly removed by digestion. They are essentially long, narrow tubes with relatively infrequent cross septa. Septa and walls are water impregnated, and the lumina are at first filled with water (aqueous solution) and eventually with gas as they become old. Many other kinds of dead cells, generally filled with gas, occur in old stems, such as trees. Other chambers besides living and dead cells are the intercellular spaces, usually gas-filled also. These are formed by splitting of walls and pulling apart of the two resulting layers. Intercellular spaces are in many cases very extensive and complex in form as a result of the "running together" of many adjacent spaces. They may open to the exterior, as through stomata and lenticels. The cavities of dead cells and of intercellular spaces may be joined by the disappearance of a portion of wall.

Liquid water is seen to be continuous throughout the plant excepting for the gas-filled chambers, which are somewhat like gas bubbles in a free liquid; only they are held in position and size and form by the relatively rigid water-impregnated walls about them. Where several gas-filled spaces are adjacent the imbibed water held in the intervening walls is of course in vapor-pressure equilibrium with the water vapor of contiguous cavities. These walls are not nearly dry, excepting when their pores are largely filled with wax-like substances. The plant is therefore, as I have said, essentially a mass of liquid water held in a characteristic nexus of porous cell walls by the attractions of imbibition and osmotic pressure. It retains its form in spite of the influence of gravity, wind, and other deforming agencies, mainly through turgor in the young parts, but in thick walled tissues through mechanical resistance of wall material. Turgor involves the tensile strength of the walls and their tendency to contract when slightly stretched by outwardly directed turgor pressure; this is generally osmotic but may be partially imbibitional if the swollen protoplasmic gel acts, as a swelling colloid, to stretch the walls. In some older tissues (like wood and sclerenchyma; consider ordinary wood and the stone-cells of the date seed, etc.) the very thick walls themselves resist compression as well as other forms of deformation to a great degree.

In tissues of thin-walled living cells

(such as celery or rhubarb petioles and young leaf blades, as well as many kinds of mature leaves and even stems, fruits, etc.) the whole structure shrinks markedly and droops when turgor disappears. We say the tissue wilts under these conditions. Wilting properly begins when the cell walls cease to be stretched by turgor pressure. It may be brought about in either of three ways: (*a*) By depletion of the osmotically held water in the cell vacuoles (in which case the volume of the osmotic solution decreases, its concentration and osmotic value increase, but the actual osmotic pressure, or turgor pressure, decreases). (*b*) By the removal of osmotically active solutes from the vacuolar solution, as when sugar is converted into starch and water (in which case the osmotic value of the vacuolar solution decreases and consequently the turgor pressure that tends to stretch the walls). (*c*) By the escape of osmotic solution from the vacuoles, as when the protoplasmic cell lining becomes more permeable to some or all of the osmotically active solutes (in which case the turgor pressure decreases, although the osmotic value of the solution may be unaltered; an illustration may be had by killing the protoplasm in a turgid leaf, as by boiling).

Through the imbibition water of the peripheral cell walls the water mass of the plant is in direct contact with the environment, and water (and substances soluble in water) may enter the plant or leave it across these interfaces. According to the nature of the external walls, whether cuticularized or not, etc., the interchange of water between the plant body and its surroundings may be very much hindered (cuticularized, suberized, etc., walls) or may be relatively free (walls of substomatal spaces, root hairs, etc.).

Also the cell walls throughout the plant interior vary in water content and in the resistance which they offer to the movement of water through them, but all are impregnated with water. As to the chambers, all living cells exhibit continuous water from wall to wall, as do also many kinds of dead cells, especially the vessel segments while they are relatively young. Because of the continuity of liquid water, a solute particle might enter the plant at any point, by becoming dissolved in the pore water of an external wall, and might then diffuse across walls and water-filled cavities to any other point in the plant, remaining all the time in solution. (Such a particle might pass out of solution at some point on the periphery of a gas-filled space, diffuse across the space as a gas particle, and enter the liquid phase again at another point on the periphery of that space.) Such diffusion of dissolved substances may occur slowly from any part of the plant to any other part, provided none of the colloid layers encountered are impermeable to the diffusing particles.

But the resistance or retarding effect of the innumerable colloid layers (water-impregnated porous walls and the protoplasm of turgid cells) is very great, and diffusion from place to place in the plant must therefore be very slow indeed, much slower than would be the case in perfectly free liquid water. Solute diffusion through free water is itself very slow, but what appears as diffusion in that case is generally greatly accelerated by convection currents in the liquid. Such currents, which result in more rapid mixing, are known to occur visibly in many living cells (protoplasmic streaming) and they probably occur commonly in water-filled spaces throughout the plant body.

When water particles migrate by diffusion each particle moves on its own, as it were, like the particles of a solute. When

water moves by mass streaming it carries with it its dissolved particles—the solution flows as such—but mass flow through a colloid layer that retards some of the solute particles may leave those particles behind, the layer acting like an osmotic filter. It therefore follows that, for a given difference in hydrostatic pressure between two regions of the plant body, mass streaming, or molar flow, can occur at a given rate only if the pressure difference is great enough to overcome the resistances that lie in the path of movement. With great pressure differences water may move rapidly through paths where diffusion itself might be more rapid than flow if the hydrostatic-pressure difference were not so great. The rate of flow is dependent on the magnitude of the pressure difference and on the amount of resistance encountered in the path of movement. There appears to be no doubt that both flow of water and solution and diffusion of water and solutes occur continually in the plant, tending always to equalize hydrostatic and osmotic differences between different regions, but always hindred by walls and protoplasm.

WATER USE AND WATER LOSS

The mention of hydrostatic gradients leads to the query: how do any regions come to have lower hydrostatic pressures than the tissues of the thoroughly soaked seed or than the absorbing walls of the root system when submerged? In the first place, we have seen that enlargement occurs because of the formation or accumulation of imbibing and osmotically active substances and structures in the enlarging tissues. These become relatively drier because non-water materials continually increase in them. They consequently receive water from the other regions, eventually from the saturated regions of the roots and the solution beyond. Water taken into enlarging cells may be called *growth water*. For rapidly enlarging tissues it must be supplied at a considerable rate.

We have also seen that water is used up chemically in the living cells; it is combined with carbon dioxide in illuminated green leaves, it is combined with the component atomic groups of substances undergoing hydrolytic splitting (as when starch and water produce glucose under the influence of enzym catalysis). Water so used may be called *metabolic water*. The rate of water supply required for metabolic processes is perhaps generally lower than that required for enlargement. But, as has been seen, metabolic processes involving water in chemical ways occur also in the reverse direction; respiration produces water and the reverse of hydrolytic splittings does the same (as when glucose polymerizes to form starch and water).

Solution is sometimes excreted or secreted from living tissues by gland action, the colloid chemistry of which is not yet well understood. Water leaving the plant in this way may be called *secretion water*. The rate of such secretion is probably sometimes as great as the rate at which growth water is used. Guttation and nectary secretion are examples of this process in healthy plants. A similar process, called "bleeding," is especially pronounced in the case of tissues wounded mechanically or by fungi, etc., in some plant forms. It may be temporarily caused by decrease in the resistance to internal hydrostatic pressure, as when walls are ruptured or digested.

Guttation, which is superficially analogous to perspiration and the secretion of water on the surfaces of mucous membranes in the human body, may be readily observed at the leaf tips of young grass plants such as wheat and oat seedlings, also at the margins of leaves such as those

of the garden nasturtium (*Tropaeolum*), Fuchsia, etc. The very dilute solution forms droplets and drips off or runs down on the outside. Guttation occurs generally only when the water supply to these tissues is very high and the rate of water loss or use in other ways is very low. A secretion very similar to guttation occurs sometimes in the interior of the plant body, where solution is forced from living cells into intercellular spaces or into dead cells. Spaces or chambers usually gas-filled may thus become partly or entirely filled with liquid. When this occurs in leaves we say they are injected, but many cases of injection occur by the inward flow of water through stomata during periods when the external leaf surface is covered with superficial water. Excretion of solution from cell vacuoles into neighboring intercellular spaces is apparently the immediate cause of the local and rapid decrease or disappearance of turgor in special tissues that exhibit quick mechanical movements, as in sensitive stamens (barberry), sensitive leaves (*Mimosa*), etc. Sap pressure, root pressure, etc., when they occur in uninjured tissues, may be closely related to this sort of active secretion. I shall revert to sap pressure farther on. Wound excretion is illustrated in the Mexican century plants ("mescal"), from the extruding liquid of which fermented and distilled beverages are prepared. It is also seen in the coconut and other tropical palms, which supply similar juices that are used in similar ways.

Nectaries are common on floral parts and leaves of many plants. From floral nectaries the amount of excretion of water is generally comparatively slight, but foliar nectaries sometimes behave much like guttation glands.

After all these things have been considered, however, the most important water requirement of most ordinary plants, and of our experimental plant with its roots in solution and its foliage in the air of an ordinary room or greenhouse, is the requirement of *transpiration water*. The superficial walls of leaves and stem are exposed, unlike those of the roots in their usual environment of moist soil, to the atmospheric gases; they are not generally covered by liquid water. At these surfaces the water mass of the plant distinctly terminates, and each water-plugged ultra-microscopic pore, where its outer opening is in contact with gas, has a tiny water-air meniscus. It is through these menisci at the outer openings of colloid pores that the water of our plant is in direct contact with the surrounding atmosphere, as we have seen. When intercellular gas-filled spaces are not at all injected their peripheries present the same picture. The pores and their menisci may be less frequent and smaller (cuticle) or more frequent and possibly larger (walls of intercellular spaces like those connecting with the stomatal openings). In the latter case the menisci may be continuous laterally with a very thin superficial film of liquid that bridges the intervals between the pores. There is always such a film of adsorbed water, but its comparative immobility renders it negligible, for it acts much like the solid material that holds it.

Now, wherever liquid water or aqueous solution is in contact with gas there must occur either vaporization or condensation. Speaking more carefully, both must occur but one is generally more rapid than the other. Since the air about the leaves of our plant is seldom saturated with water vapor to the point where condensation would surpass vaporization, it follows that there is generally considerable loss of water by evaporation from the exposed menisci. This is transpiration. Transpiration water does not

leave the plant as a liquid, it vaporizes as it leaves. Transpiration tends to dry the exposed walls, to make the menisci retreat deeper into the wall pores. But they do not generally retreat to any considerable extent, for new water moves continually into the drying walls from the interior of the plant, and consequently the outer walls do not really become more than incipiently dry. The rate of transpiration is generally high, much higher than that of all other water losses and water uses combined, and one of the main requirements for plant health is generally the necessary supply of water that replaces transpiration loss. This consideration is at the base of all agricultural irrigation.

Water must be supplied to the absorbing roots a little more rapidly than it is lost by transpiration, or else the water mass of the plant must shrink. If it shrinks the first notable effect is to reduce the turgor of living cells in some regions, which actually wilt if turgor pressure becomes zero. Enlargement cannot proceed without turgor, and growth ceases before wilting begins. But some parts of a plant (as the older leaves) may lose turgor, wilt, die, and dry up, while other parts (as growing tips) are still turgid and growing. This is partly because water movement through the tissues along some paths is so hindered by resistance that the drying cells may die and become filled with gas in spite of the fact that there is slow movement into them from other parts. The occurrence of wilting in some tissues before it occurs in others is also partly due to differences in turgor pressure.

It should be noted that the transpiration rate must become zero when evaporation from the air-exposed surfaces ceases, especially when the leaves are covered with a layer of liquid water, as in long rainy periods. Conditions that promote the formation of dew on leaf surfaces to a standstill. At such times leaves and stems may absorb some water, just as do the roots in our experimental solution culture. But the possible rate of water absorption through leaf and stem surfaces is very low, for cuticle, cork walls, etc., contain but little water when fully saturated, and water movement through them is correspondingly slow for any pressure differences that occur.

Another observation of importance in some cases is this, that one portion of a plant may shrink and give up its water to other portions, although the cell walls remain at first impregnated with imbibition water. This suggests another internal source of water for growing tissues. Since the water here referred to is characteristically set free through the wilting of tissues we may term it *wilting water*. It is, in a sense, the reverse of growth water. In periods of great aridity, of high transpiration rates and low absorption rates, some parts of the plant may maintain health and growth partly or wholly at the expense of water previously held for a long time in the cells of other parts. A massive cactus plant may blossom and produce fruit annually for several years without any entrance of water from without. In the meantime the water-storage tissues shrink and eventually die, even the intervening cell walls being largely oxidized, thus adding some metabolic water to the wilting water removed. Transpiration continues slowly, and yet new growth occurs each year, in the production of blooms and even rather juicy fruits. Partly developed fruits of plants like the orange may be thus sacrificed in times of drought. Succulent plants like the live-forevers (*Sedum*, for example) may grow for weeks in a plant press unless the protoplasm has been killed by immersing the specimens in boiling water before placing them in press.

water supply and water requirement as follows:

Water requirements	*Water supplies*
Growth water	Wilting water
Metabolic water	Metabolic water
Excretion water	Water absorbed through leaf surfaces, etc.
Transpiration water	Water absorbed through root systems.

For general purposes we may neglect all forms but the last in each category. The main water requirement of most ordinary plants is transpiration water, and the main supply comes through the absorbing surfaces of the root system. We shall now consider the general mechanics of root absorption and transpiration a little more closely.

WATER ENTRANCE THROUGH ROOTS

The root system of our experimental plant is in a nutrient solution, and the outer walls of roots and root hairs are in direct contact with the surrounding liquid. The water mass of the plant is therefore continuous through these walls with the solution on the outside. There is no external resistance to the entrance of water into these walls from without. We neglect the slight osmotic resistance due to solutes in the nutrient solution that are not able to pass into the walls as rapidly as water does; such resistance is negligible when the nutrient solution is sufficiently dilute (when its osmotic value is of an order of magnitude of 0.1 atmosphere or lower). The rate of entrance of water through the roots of our plant must consequently be determined by conditions effective within the body; the weak solution can supply water to absorbing root surfaces as rapidly as absorption may occur, even though some of the solute particles of the medium may be shut out by osmotic or electric conditions. The water-supplying power of such a liquid medium is practically without limit, so long as the medium bathes the absorbing surfaces.

TRACTION IN LIQUID WATER

It was said above that one particular physical principle has recently come to appear fundamental in our conception of plant water relations. I referred to the capacity of water, aqueous solutions, and other liquids to transmit traction. This property of liquids has long been known, but it is generally neglected in treatises where one might logically expect to find it discussed. Most physicists and plant physiologists now appear to have but a vague appreciation of this characteristic of water. We may here consider it briefly from the physical point of view and then turn to its importance in plant physiology.

Water, mercury, and other liquids exhibit a high degree of cohesion but a low degree of viscosity, as compared with solids; we suppose that their particles are strongly attracted to one another but move upon one another with but very little resistance. It is therefore easy for some minds that have not become thoroughly familiar with the experimental and theoretical evidence, to regard the transmission of traction through a mass of liquid as no more than a myth. But the tensile strength of liquid water and weak aqueous solutions amounts to at least several hundred atmospheres. This may be deduced from other characteristics of water, and the phenomenon of taut water may be readily demonstrated experimentally.

The demonstration may conveniently follow the method of Berthelot or that of Böhm and Askenasy. In both cases a rigid wall is provided for the experimental water mass, of glass, porous porcelain, wood, etc., and precautions are taken to

insure at the outset thorough adhesion between the wall and the liquid. Gas bubbles of considerable size must be avoided, but dissolved air in the water does not hinder successful demonstration.

By the Berthelot method, much improved in detail by Dixon, a closed glass tube some 30 cm. long and nearly filled with water is carefully heated till the water expands and completely fills the cavity, while the originally enclosed air goes into solution. The whole is then cooled. The liquid tends to contract on cooling, but it adheres so strongly to the glass walls and its cohesion is so great that it remains filling the tube completely at a much reduced temperature. Under these conditions the water mass is actually stretched, which demonstrates the presence of traction strain. Dixon reports an experiment in which a mass of water at 72.9°C. occupied the volume natural to it at 84.9°C., a stretching amounting to 158.4 atmospheres of pressure. The hydrostatic pressure in the stretched water is negative and numerically equivalent to the stretching strain. The liquid is greatly supersaturated with air, and yet no bubbles form. The water mass finally ruptures as the temperature is lowered, when a pronounced click is audible.

By the method of Böhm and Askenasy the demonstration is even more striking, though the magnitude of the strain produced by this procedure is thus far only of the order of an atmosphere or two. Böhm employed a cut twig of arborvitae suitably joined to the upper end of a vertical glass tube filled with water. The lower end of the tube dipped into mercury below. Transpiration from the leaves caused the mercury to rise to a height of about 90 cm. above the mercury level in the reservoir. Since the atmospheric pressure on the reservoir meniscus (equivalent to somewhat less than 76 cm. of mercury column) could not support the liquid in the tube to such a height, it is clear that the water in the twig and in the tube, as well as the mercury in the upper portion of the latter, were actually supported by a pull from above, not by a push from below. Askenasy's classical experiment is like Böhm's, but Askenasy used a funnel filled with solidified plaster of Paris instead of Böhm's twig. In the hands of later workers the funnel and plaster are replaced by a porous porcelain plate or bougie suitably attached to the tube, as by means of a rubber stopper. A modification of this experiment, with special procedures that make success with it almost certain, has been recently described in the third American edition of Palladin's Plant Physiology, and a succinct account of the main aspects of the physics involved has been given by Livingston and Lubin in *Science* for April 15, 1927.

The pores of the porcelain are plugged with water, and the air-water meniscus at the outer opening of each pore is held fixed by capillary forces resulting in an imbibition pressure capable of withstanding an excess of several atmospheres of external air pressure. It is these pore menisci that prevent the entrance of air, just as in the case of the pore menisci of the outer walls of the leaves of Böhm's twig. Undissolved air cannot enter the system until one or more of the water plugs have been forced inward through the wall. But water evaporates from the pore menisci, as in the case of the external walls of plant leaves, and the hydrostatic pressure within the bougie and tube is consequently decreased. The water column shortens as evaporation proceeds, and mercury rises in the tube from below, replacing the water lost above. The hydrostatic pressure at the mercury-water boundary decreases progressively

as the boundary ascends, becoming zero when the column of mercury just balances the opposed external pressure due to the atmosphere acting on the mercury-air surface in the reservoir. At this time the pressure at every level in the mercury is positive, being greatest at the bottom and zero at the top of the column, and the pressure at every level in the water is negative, the negative value being greatest at the top of the system and zero at the mercury-water boundary. With the continuation of evaporation from the bougie and the consequent farther ascent of the mercury-water boundary, the pressure in the upper portion of the mercury also becomes negative.

By the Askenasy method it is possible to demonstrate an atmosphere or more of negative pressure at the top of the system before the column ruptures. (Why it ruptures in this experiment is not understood. Nothing approaching the tensile capacity of water or mercury has yet been shown in this way, but this method is more suitable to demonstrate the principles involved than is the Berthelot method, although that gives very much greater strains.)

The liquid having negative pressure is really slightly stretched, as in the Berthelot experiment. The water adheres to bougie wall, stopper, tube, and mercury, and the whole upper portion of the liquid mass hangs on the practically rigid walls just as the water mass of Böhm's twig does when negative pressure has been developed by transpiration. The negative pressure is an inward pull on all walls.

One further consideration in regard to the Askenasy experiment requires special attention. In the earlier stages, before negative pressure has appeared at all, the ascent of mercury in the tube is of course due to the pressure difference between the outside and inside of the system, but both pressures are positive and the difference is positive. In these earlier stages the experiment demonstrates suction but not tension in the liquid. As every one knows, the limit of suction is the current atmospheric pressure, as shown by a barometer. The continued rise of the mercury column beyond the height representing the magnitude of the current atmospheric pressure *appears* to show the development of a sort of super-suction, but the word suction should not be employed where traction is meant. In suction the moving liquid is affected by two opposed but unequal pressures, both tending to compress the liquid. In traction also there are two opposed and unequal pressures, but both tend to overcome the cohesion of the liquid and thus stretch it. In suction the liquid is *pushed* up; in traction it is *pulled* up. In suction the enclosing walls are pushed inward by positive pressure of the atmosphere; in traction they are not only thus pushed inward but also pulled inward by the negative pressure in the liquid. In these experiments traction does not begin to be manifest until the possibilities of suction have been surpassed.

PRESSURES IN THE PLANT

Turning once more to our experimental plant, with its roots in aqueous solution and its stem and leaves in air, and keeping the Askenasy experiment in mind, we readily appreciate why the water lost by transpiration, etc., or used in growth or metabolism, is generally replaced by water entering through the root surfaces. The whole plant corresponds to the bougie and tube of the Askenasy apparatus, but it is water that enters below instead of mercury. As transpiration water leaves the foliar surfaces, to use the most striking example of water use or loss, the hydrostatic pressure within the plant is cor-

respondingly reduced, and water movement occurs from the root surfaces to the leaf surfaces, mainly along the paths of least resistance; that is, through the vessels, which extend from root to leaf. The upward stream flows around enclosed gas-filled spaces and regions of too great resistance, but the strain tends always to extend throughout the entire water mass and in all directions. The gas masses of enclosed spaces expand as much as possible, but their expansion is checked by their surrounding water-plugged walls. This applies to gas-filled vessel segments as well as to intercellular spaces and ordinary cells that contain undissolved gas. The gas pressure in such spaces is low, but it is of course positive in sign; considerable negative pressures do not occur in gases under ordinary conditions.

If our plant is only a few centimeters high and if the transpiration rate is not too rapid, entrance and movement of water may be wholly accounted for by suction, but with higher rates of water loss suction alone can not make good the deficiency, and negative pressures are then developed in the water mass of the plant. If the plant is tall enough to have its water mass higher than the water-barometer column (about 10 meters), negative hydrostatic pressure and liquid strain must have been developed in its upper portion by growth alone, without considering rates of upward movement of water or resistances at all. It is very doubtful whether ordinary plants, even very small ones, could develop or exist in natural environments if it were not for the capacity of water to transmit traction pressure of many atmospheres when held in the colloid-osmotic structure typical of all plant bodies.

If the plant is of low stature, if the transpiration rate is low enough, and if the roots are covered with liquid water, traction will not occur. This case corresponds to the earlier stages of the Askenasy experiment. The inwardly directed, positive pressure exerted on the periphery of the plant body by the atmosphere tends to move the outer walls inward, to overcome the turgor pressure of superficial cells everywhere (thus tending to cause their collapse and the extrusion of their contents), to compress all cell walls, imbibition water, and the whole water mass of the plant, and to decrease the volume (and increase the gas pressure) of all enclosed gas-filled spaces. This is opposed by the turgor pressure of the outer living cells and by the resistance of the liquid and of the cell walls to compression. When some water is removed from the mass at any point (as by growth, metabolism, transpiration, etc.), the internal hydrostatic pressure is decreased and the plant body tends to shrink, but water enters through the roots and makes good the loss. Without the development of liquid strain (hydrostatic pressure of negative sign), however, the difference between the general internal pressure and the external pressure can never exceed about one atmosphere; for the internal pressure cannot thus be lower than zero and the external pressure does not exceed about one atmosphere under natural conditions.

If, however, the plant is taller than the suction column of water, or, even when it is of low stature, if the transpiration rate is sufficiently high in relation to the rate of water absorption by the roots and that of conduction to the leaves, then liquid strain occurs in at least portions of the water mass. Since water adheres very firmly to the peripheral walls, this negative pressure is numerically added to the atmospheric pressure; the inward pull is added to the inward push.

The turgor pressure (largely osmotic)

of the cells needs special attention. This tends to keep the cell walls stretched sufficiently so that their elasticity results, for each cell, in an inwardly-directed pressure equivalent to the turgor pressure. Each turgid cell occupies as much space in the water mass as the elasticity pressure of its stretched walls permits. Turgor pressure is generally of a magnitude between about 3 and about 15 atmospheres, but it is greater than 100 atmospheres in some leaves, etc., of plants grown in arid habitats.

Excepting at the periphery of the plant and at the periphery of gas-filled spaces, however, turgor pressure is without direct influence on the general hydrostatic pressure of the water mass, for it is opposed and equalled, for each turgid cell, by the elasticity pressure of the wall. Consequently it is local. In the interior of the water mass, a turgid cell is not unlike a closed rubber bag distended by water that has previously been forced into it, the bag being completely submerged in a large tank of water. The hydrostatic pressure of the tank is clearly independent of the turgor of the bag. Although fluctuations in turgor pressure in interior cells are without influence on the general hydrostatic pressure, still they must tend to produce shiftings of the wall positions, just as the wall of our rubber bag would change its form and position in the tank if we were to force more water from the tank into the bag or let some of the contained water out of the bag into the surrounding liquid mass.

For peripheral cells the relations are very different, since water may here escape from or enter the entire system, but undissolved gas cannot enter. If water is removed from such a cell, and not replaced, its flexible outer wall moves inward, the volume of the general water mass being correspondingly decreased. The inner walls move outward a little also and there may be many slight shiftings of walls in the plant interior. If water removal continues sufficiently long, without corresponding replacement, these cells collapse, turgor having disappeared. To bring this about with nothing but positive pressures it would of course be necessary that the environmental pressure should be greater than the local turgor pressure. This rarely if ever occurs, but internal traction is added to the environmental pressure. The removal of water from the plant at any place, within or at the periphery, decreases the volume of the general water mass and results in shrinking or wilting of peripheral cells unless water enters the body in equivalent volume. It is to be noted that the category of peripheral cells includes all living cells abutting on internal gas-filled chambers, as well as those under the direct influence of the outer air pressure.

Hydrostatic pressure, whether positive or negative in sign, is transmitted equally in all directions throughout the liquid mass, and water movement between peripheral cells and the rest of the system tends to equalize differences of pressure, as has been seen. Thus some peripheral cells wilt, collapse, and die, while others, because of higher turgor pressure or greater resistance to collapse on account of wall strength, may maintain their volumes. Leaves may wilt while growing points are still enlarging, etc. Transpiration from leaves tends to produce wilting not only in leaves but also in all peripheral cells, as in root hairs not externally in contact with water that may enter under the influence of a pressure less than their turgor pressure.

In the case of gland action solution may, as we have seen, be pressed out of the cells, traversing the cell walls. It may (*a*) pass to the outside of the plant, (*b*) pass

into a previously gas-filled space, or (c) simply pass into the general water mass of the plant, in which case the result is merely a shifting of cell walls. Gland cells must, however, derive their secretion water from the general water mass or else from the outside, through externally wet peripheral surfaces. If water is adequately supplied through the roots a gas-filled space may become filled with liquid, or solution may be actually extruded from the plant, without necessitating any shrinkage of the water mass or collapse of any peripheral cells. But without adequate water supply such liquid movement must have the same general results as that produced by transpiration.

Like osmotic pressure in individual cells, gland action in the interior of the water mass may result in the local development of hydrostatic pressure higher or lower than that of the system in general, but, as has been said, such local pressures must be without influence on the hydrostatic pressure of the water mass in general, as related to the exterior. Local internal secretion has been made much of by many writers on the movement of water in plants, but hypotheses that involve secretion as an essential feature of the general movement all fall to the ground when subjected to physical analysis with due regard to the pressure and energy relations and to all the facts that are known. There is no doubt that slow local movements from place to place in the plant may in many cases be referred to active secretion, just as guttation and the excretion of nectar are so referred, but the general flow of water from roots to leaves appears to be explained without any direct reference to such so-called vital action. (It is highly probable that the phenomena of secretion or excretion may soon be explained by reference to colloidal and osmotic phenomena, but this is not the place to attempt any analysis of the possibilities of the case. To mention the phenomena of coagulation, alteration in pore size, syneresis, may be suggestive. When the physics of secretion becomes better understood that advance will surely remove another prop from vitalistic thinking.)

Consider now the hydrostatic pressure just within or behind the water-air menisci that close the pores in an exposed, water-impregnated wall of a turgid cell, such as the wall of a substomatal space. The pressure of the atmosphere is not sufficient to force the liquid plugs from these water-plugged pores and therefore undissolved air cannot enter. The external walls are supported by turgor pressure. Removal of water by transpiration, etc., results in a pressure at the point in question lower than that exerted on the external water in contact with the absorbing root surfaces. It is the difference between these two pressures that produces inward or upward flow. If the smaller, inner pressure is positive the difference, as we have seen, cannot significantly exceed one atmosphere. If the inner pressure is negative (the liquid being then in a state of strain) the difference may amount to many atmospheres, depending on the negative magnitude. In general, the atmospheric pressure on the exposed walls, plus any traction that may be present in the water mass, results in a pressure tending toward collapse of peripheral cells and enlargement of the gas spaces. This outer push and inner pull tend to reduce the volume of all water-filled parts. But to the resultant pressure is opposed the rigidity of the colloid and osmotic system. This rigidity is partly due to the ordinary mechanical strength of cell walls, but in active tissues (with thin walls) it is due mainly to turgor. It is the turgor of the leaf

parenchyma alone that prevents the collapse of these cells. A peripheral cell can maintain turgor only so long as its actual osmotic and imbibition pressure is greater than the sum of atmospheric pressure and whatever traction exists in the water mass of which these cell contents are the outer part. If the turgor pressure is surpassed these cells collapse and the leaf wilts. If the pressure difference continues to increase, air finally finds its way into cells, vessels, etc., the water plugs in the larger pores of the walls being the first to give way unless the collapsing walls are actually torn open. Such cells play no further part in the water mechanics of the system, excepting that they act to retard water loss from the deeper, still living cells.

We thus see that turgor pressure in thin-walled cells is highly important in maintaining the water mass of the plant without too great decrease in volume or other alteration in form that would destroy it as a mechanism. It used to be thought that osmotic attraction might somehow play an important and immediate part in the entrance of the water stream through root surfaces and in the flow of the transpiration stream, but hypotheses on that basis must be laid aside, although they are still commonly presented in vague and unsatisfactory ways in text books of plant physiology. Osmotic pressure of peripheral cells is of fundamental importance, but not directly; it practically sets a limit to the magnitude of the motivating pressure difference (mostly traction) that can develop in a plant.

What has been said about leaf parenchyma applies also, *mutatis mutandis*, to all thin-walled living cells throughout the plant body. Turgor pressure, whether due to osmotic pressure or to imbibition pressure, tends to maintain the form of the living cells in the body; that is, it tends to maintain the relative positions of the walls. It is essential to enlargement. The maintenance of turgor and form in living cells is doubtless generally essential to their metabolism as well as to the rigidity of peripheral tissues.

Special attention needs also to be given to the pressure relations of enclosed gas-filled spaces in the plant body. These were all originally parts of the liquid continuum, but their liquid contents have disappeared. Suppose an intercellular space nearly filled with water but containing a small gas bubble; where gas has come out of solution or where the taut water has been torn apart, for example. The bubble expands till its gas pressure and surface tension combined are just balanced by the hydrostatic-pressure difference between the surface and the interior of the water system in general, provided that this difference is not greater than the gas pressure and surface tension of the bubble when fully expanded so as to occupy the entire intercellular space. Such gas pressures in enclosed spaces can never be below zero, though they may rise to much above a single atmosphere when such a gas as carbon dioxide is actively discharged into these spaces from the surrounding liquid surfaces. Before the surrounding liquid becomes stretched (negative pressure) all free liquid has left the spaces, and their walls are like the outer ones of peripheral cells exposed to the atmosphere. These walls are then pulled outward, as has been seen.

As the longitudinal rows of cells forming the vessels mature many of the cross walls get dissolved and the protoplasm disappears, but the resulting tubes remain filled with liquid, and this transmits hydrostatic pressure in all directions. If a gas bubble of considerable size forms in a vessel segment, as by rupture of the

stretched water, it expands till that segment is completely filled with gas. Here again the taut water pulls the walls outward because it adheres in the pores. In some forms some of the vessels continue filled with water for years while the lumina of other vessels may be removed from the liquid system after a much shorter time. Many of the older vessels of the trunk of an old tree are thus gas-filled. Indeed, the whole interior of the trunk may decay while the tree remains healthy as a whole.

Water moves about the plant in all directions, in accord with hydrostatic-pressure gradients, always flowing most rapidly along paths of least resistance, as we have seen. Water removal is mainly at the top and water entrance at the bottom; consequently the most rapid movement is, in general, upward from root to leaf. Although lateral flow of water from one vessel to another at the same level generally encounters greater resistance per unit of distance traversed than does upward flow (for more walls must be passed, and often, also, the water masses of living cells), yet lateral movement occurs commonly enough to allow the stretched water to flow upward around the gas-filled segments in conducting bundles. Movement occurs wherever traction is developed, but it is slow or rapid, for a given amount of traction, according to the resistance encountered.

Old vessels that have become gas-filled do not generally become again filled with liquid, it seems, excepting possibly in plants of very low stature. New vessels are continually forming in the youngest regions of the tree trunk, however, and the number of water-transmitting vessels increases as the tree increases its diameter, in spite of the continual loss of transmitting vessels in the older parts of the xylem. We may say that the taut water strands of the vessels "wear out." It appears that they are not generally rejuvenated but that their rôle is taken over by newly formed ones.

It still remains an open question, however, whether gas-filled vessel segments in a conducting bundle may not sometimes become once more filled with water. If this occurs in the upper parts of tall trees it must be due to some special gland action of living cells. It is conceivable that sap pressure may sometimes inject liquid into a segment previously emptied of all but gas, at a rate rapid enough to result in bringing that segment back into the water system of the plant. This point requires further study, but all features of the rise of water in plants are generally cared for if we make the supposition that no vessel segment that has once lost its liquid is ever refilled. In other words, we may tentatively suppose that if the taut water mass is ever broken in a vessel segment it is never replaced, that segment remaining a gas space, an island in the water mass.

ROOTS IN SOIL

We may now examine the results of a complete cessation of water entrance through the roots, for which purpose we may imagine that we have transferred the root system of our plant to water-saturated air. We suppose that the leaves are still exposed to ordinary air and that transpiration continues. The film of solution adhering to the roots is soon absorbed, and ultra-microscopic air-water menisci are then formed at the outer openings of the pores of the peripheral root walls, just as in the case of walls bounding substomatal spaces in the leaf. The water mass of the plant is now completely bounded by water-plugged walls and is in contact with gas at the outer surfaces of these walls. But the periph-

eral water menisci are so strongly held in the wall pores by adhesion and surface tension that it would require many atmospheres of gas pressure to force them inward. However, as we have seen, outside of laboratory procedures the gas pressure is never greater than about one atmosphere.

Since the roots of our plant are bathed in water-saturated air we may assume that no evaporation occurs from their surfaces, but neither can water enter (unless possibly a negligibly small amount of condensation may occur). (If the air about the roots were unsaturated transpiration would occur from the root surfaces as well as from the aerial parts.) Transpiration from the leaves continues to reduce the volume of the water mass, and the inner pressure decreases gradually; that is, being negative in sign, its numerical value increases. Eventually the inward traction becomes greater than the turgor pressure of peripheral living cells, the latter decreases to zero, and wilting occurs. The first cells to wilt may be those most exposed to evaporation in the leaves, but the traction in the liquid mass of the plant being transmitted in all directions, the root hairs and other superficial cells of the roots very quickly come to the same condition; wilting of delicate roots, under our experimental conditions, occurs almost as soon as wilting of leaves. It should be added that tissues with exceptionally high turgor (due perhaps to a large sugar content and a resulting high osmotic pressure) should resist wilting when the tension in the general water mass is sufficient to produce the collapse of cells with lower turgor pressure. It thus comes about that not all parts of a plant show the onset of wilting at the same time or with the same negative pressure in the vessels, etc. If a high transpiration rate is maintained (as with leaves exposed to sun, warm air, and wind) most of the outer peripheral tissues of the plant, including all the younger roots as well as the leaves, eventually wilt, break their water continuity with the remaining parts, and dry up.

Let us next consider the condition of roots in an ordinary soil, containing a considerable amount of water (soil solution). The young roots and root hairs growing into new regions are at first surrounded by at least thin layers of solution, and absorption goes on as though the roots were in free liquid. Water is of course required for root enlargement, and some of the water taken up may therefore be fixed in the new root tissue. It seems probable that roots may sometimes push considerable distances into a region of the soil that does not supply enough water for even this growth, the soil-water films being too thin; in such cases the growth water of the advancing roots must be drawn from other roots, which may be in wetter regions, or perhaps from water previously stored in other parts of the plant body. Such roots might be growing in the soil air, which is generally saturated or nearly saturated with water vapor.

With wet soils absorption of liquid water may continue for some time, but it eventually ceases unless water is added to the earth about the roots, as by rain, subterranean flow, or irrigation. Water moves but slowly through soils that are not very wet, and it now appears that root surfaces do not draw water from any great distances in the soil. They nearly dry the layer adjacent to them, and they continually advance into unexplored regions.

The outer cells of the roots of many kinds of plants grow out to form root hairs, which apparently occupy very thoroughly a cylinder of soil around the root, to a distance of a centimeter or so.

Root hairs are short lived; apparently their collapse and death are in many cases brought about by internal traction when the adjacent soil-water films are depleted and absorption ceases. They are very delicate, very thin walled, and they do not generally last long in any event. There seems to be no doubt that root hairs, when present, act as absorbing surfaces, but they are not essential, for many plants grow well without them and many forms never produce them.

The zone of root hairs, a little behind the root tip, proceeds forward with the advance of the tip itself, and, in merely moist soils, the soil films with which contact is made give up most of their water. If this be a true picture, a plant rooted in a not very wet soil would soon succumb to inadequate water supply if root enlargement were to cease. It seems that numerous fine rootlets and their branches, often provided with root hairs for a period, are continually sewing the soil mass through and through, picking up soil solution as they come to it, somewhat as a vacuum cleaner picks up dust. Before root growth is completely checked most of the water originally present has been absorbed from the whole soil region through which the root system has been operating, provided of course that all other conditions that influence root growth and absorption of water are adequate.

SOME MAGNITUDES AND RATE RELATIONS

As to the magnitudes involved in the phenomena we have been considering, the turgor pressure of living cells in ordinary plants amounts to, say, from 1 or 2 to 12 or 15 atmospheres. In the leaves of desert plants it may exceed 100 atmospheres. Imbibition pressure appears to be low usually, except perhaps in embryonic tissue, resting seeds, etc. When the imbibing material is nearly saturated with water, as in cell walls generally throughout the plant body, the actual pressure exerted by the tendency to swell is of course approximately balanced by the turgor pressure of the cells and may be estimated as usually amounting to from 1 to 15 atmospheres in turgid tissues. The less nearly saturated the imbibing material, the greater the swelling pressure developed by the imbibition of an additional increment of water. Dry starch attracts the first increments of imbibition water with a pressure of over 2500 atmospheres. A gelatin gel containing 28 g. of gelatin to 100 g. of water attracts additional water with a pressure of about 200 atmospheres. Ordinary porous porcelain, such as is used for filters, atmometers, etc., or for the Askenasy experiment, holds imbibed water against a gas-pressure gradient of from 1 to 5 or 6 atmospheres. (Of course such material does not alter its volume with change in its water content, and its structure is different from that of cell walls and protoplasm.) The exposed cell walls of xerophytic leaves hold their water of imbibition against pressure gradients of 100 atmospheres or more.

In the dry seed imbibition attraction appears to be very great. The first swelling of a seed may, in many cases, be largely due to imbibition pressure and the swelling pressure amounts to many atmospheres. The negative hydrostatic pressure (strain or traction) in the vessels of plants of low stature frequently attains a magnitude as great as that of the turgor pressure in the leaves, for it is common to see the foliage of such plants wilted in the middle of the day. Renner concluded, from some ingenious measurements, that the liquid strain in stems of low shrubs such as Forsythia was between 1 and 5 atmospheres. The tran-

spiration rate was low, and the soil about the roots was very wet at the time. In the tallest trees the strain near the top must be at least of the order of 10 or 12 atmospheres.

Water frequently moves upward in the xylem of plants at a rate of 30 cm. per hour or at still greater rates. Transpiration occurs from leaves at rates up to a few hundredths of a gram per hour per square centimeter of foliar surface. Root tips generally advance through the soil at rates of a few centimeters per day. Soils in which plants are beginning to wilt can generally supply less than 10 mg. of water per square centimeter of absorbing surface for the first hour of contact.

In ordinary healthy plants the rate of water absorption through the roots is about equal to the rate of transpiration; the absorption rate is a little greater by night than the rate of water loss and a little smaller by day. The transpiration rate itself is generally much greater by day than by night. As long as the soil can supply an adequate amount of water to the advancing root system the rate of absorption is determined by the transpiration rate and internal conditions, but when the supplying power of the soil is inadequate that becomes the limiting condition.

The transpiration rate is of course determined largely by the extent of the leaf surface, as well as by the nature of the peripheral walls, stomatal arrangement, leaf shape, etc. Fluctuations in the rate per unit of leaf surface in any plant are dependent mainly upon air conditions but also, in many forms, to a considerable extent upon changing size of the stomatal openings. This rate may be two or three times as great with open as with closed stomata. It is not unusual for the air conditions that influence the transpiration rate to have day values five or ten times as great as the night values. For example, if the rate of stomatal transpiration is taken as unity for a night period, with unity as the corresponding value of the evaporating power of the air, then the rate for a day period might be 3 if the evaporating power of the air remained at unity, but if this external influence had a day value of 5, the transpiration rate for the day period would be 15.

Rates of transpiration, and of absorption, may also be limited by the water-conducting power of the plant; the conducting system may be inadequate, even with wet soil. Wilting of diseased plants is often due to plugging of the vessels by parasitic fungi. It is sometimes supposed that the lowering of the vapor pressure of the water in peripheral cell vacuoles, due to the presence of dissolved substances, may be effective in retarding water loss by transpiration, but such retardation cannot be significant. Even if the vacuolar solution extended through the wall to the exposed surface, which it does not do, evaporation would be retarded less than ten per cent in the case of the most concentrated solutions ever recorded for plant vacuoles.

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MILK SECRETION AS INFLUENCED BY INHERITANCE

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MILK in general is a sex-limited product, as the secretory activity of the mammary glands is limited to females of the mammalia. The first product of milk secretion, colostrum, is striking in its composition and markedly different from that to follow. It is richer in the albumin and globulin fractions of the protein and in the salt. It contains many cells, frequently spoken of as milk corpuscles, which contain nuclear material. The fat has a higher melting point and contains more cholesterol and lecithin than the subsequent milk. Our scant present-day knowledge of this product shows that it is important in protecting the young of several species against immediate bacterial invasion. After a week or so from the time of parturition the mammary gland secretion loses the characteristic properties of colostrum and assumes those common to normal milk. As yet no data are available to investigate the relation which exists between colostrum and the secretion of a later period.

Considering the world in general, the milk used for human consumption may come from a number of different species of animals. Thus milk from cows, sheep, goats, mares, camels, etc., are all products used in the human bill-of-fare. Here in the United States almost the only source of milk and its products is the dairy cow. It is because of this fact that the available records on the amount and quality of milk are almost entirely limited to this species. The data, from which our information relative to the factors affecting milk production is obtained, are consequently confined almost entirely to dairy cattle.

Cow's milk is made up of protein, fat, sugar, and salts. The protein may vary from 2 to 5 per cent of the milk's weight; the fat from 2.0 to 8.0 per cent; the sugar from 3.5 to 7.0 per cent; and the ash from 0.63 to 0.84 per cent. The protein is largely composed of two substances, casein and lactalbumin. These substances are characteristic of milk and are, in fact, characteristic of the species giving the milk. Butterfat is also of characteristic composition, containing mainly the fatty acids, butyric, caproic, oleic, palmitic, and stearic. The sugar of milk is lactose, a product characteristic of mammary gland activity. The ash is composed of several salts, calcium and phosphorus being the predominant elements. Besides these major products there are many minor constituents of milk whose importance in the general economy of animal life is but now coming to be recognized. In other words, milk is a highly complex metabolic product.

MECHANISM OF MILK SYNTHESIS

The combined efforts of earlier investigators have given us hypotheses, imperfect though they are, to account for the mechanism by which the animal body supplies the raw material to the mammary

gland for the making of its products. As blood is the common carrier for most of the materials utilized in metabolism, it is natural to turn to it as the source of the precursors of the milk solids. The most fruitful method of analyzing what these precursors of the milk solids may be, has consequently been that of comparing the composition of the blood which is entering the mammary gland as contrasted with that coming away from it. This method of approach as first indicated by Kaufmann and Magne, in their hands and also that of Cary, has shown that the blood entering the mammary vein contains about 20 per cent more dextrose than that coming away from the mammary gland. Such being the case it is considered reasonable to suppose that the lactose, or milk sugar, is manufactured from the dextrose, or blood sugar. Meigs, Blatherwick, and Cary have utilized the same method to indicate the origin of the milk fat. They believe that the blood entering the udder carries more phosphatid than that leaving the udder; that the blood entering the udder carries less inorganic phosphate than that leaving the udder. From these two observations and the difference in the composition of milk compared to that of blood with regard to phosphorus, they draw the conclusion that the mammary gland in butterfat secretion takes phosphatid from the blood, converts it into fat, and returns as inorganic phosphorus the excess phosphorus derived from breaking down the phosphatid. Cary, following this same order of approach, shows that the blood entering the udder contains more amino nitrogen than the blood coming from the udder. From this fact and the recent work on the metabolism of protein he draws the conclusion that the proteins of milk are derived from the amino acids of the blood.

Another method of approaching this problem consists in the administration of some product which alters the composition of the blood or the general metabolism of the animal. Such a product, phloridzin, has been used frequently for this purpose. The results from its use, however, are complicated by the fact that it has broad physiological effects, not only causing a glycosuria but also markedly increasing the nitrogen elimination from the body. Another product which perhaps has more possibilities is insulin. In some preliminary experiments with this material Tobey and the writer found it possible to reduce the blood sugar of a lactating cow to three-fifths the normal. The milk of this cow was found to have slightly less lactose in it than it would normally have, roughly a reduction of 10 per cent in the total lactose. At the same time the ash showed a remarkable increase in its percentage. The other constituents were variable, varying in both directions around the normal. These results might tentatively be interpreted as supporting the conclusion that the dextrose of the blood is the precursor of lactose.

The problem before us may now be stated in physiological terms in the light of the foregoing facts. In studying milk secretion five large groups of metabolic products are dealt with: water, constituting roughly 87 per cent; sugar, 5 per cent; butterfat, 4 per cent; protein, 3 per cent; and ash, 0.75 per cent. Our present knowledge, scanty and irregular though it is, indicates that in the formation of these products the raw materials in the blood appear to be: dextrose, phosphatids, and amino acids. The problem in hand is to determine the influence of inheritance on controlling the variation in the metabolic activity of the mammary glands expressed as quantity and percentage content of the milk constituents.

Genetic studies largely limit themselves

to two major phases of this problem, the milk quantity, or the interaction of all of these variables to produce small or large yields of milk, and the butterfat percentage found in the milk. Besides these data there exists a small amount of information on the inheritance of the other milk constituents, as lactose, protein, and ash.

THE INHERITANCE OF MILK YIELD

The study of the inheritance of milk production is complicated by the fact that the metabolic activity of the mammary gland changes remarkably with the age of the animal. This change, as first noted by Pearl, is logarithmically related to the cow's age, or speaking in terms of lactation yield, the cow of two years of age gives a relatively small amount of milk. This yield is rapidly increased on the cow's second lactation at three years of age. The lactation yields continue to increase, tation, until the cow reaches her maximum production at between six to ten years of age. From this point the lactation yields tend to diminish at an ever increasing rate. Figure 1 shows graphically how this change of production takes place with increasing age for a herd of unselected purebred Jersey cows.

Figure 1 indicates the striking changes which take place in the metabolism of milk as the age of the cow increases. It further illustrates the attention which must be paid to these changes in comparing the production of cows whose lactations start at different ages. It is therefore necessary in all critical work on milk production to standardize the records to a given age or to utilize records which are made at a single age. Throughout this paper the writer has taken account of this factor age so that the conclusions are based on records standardized for age.

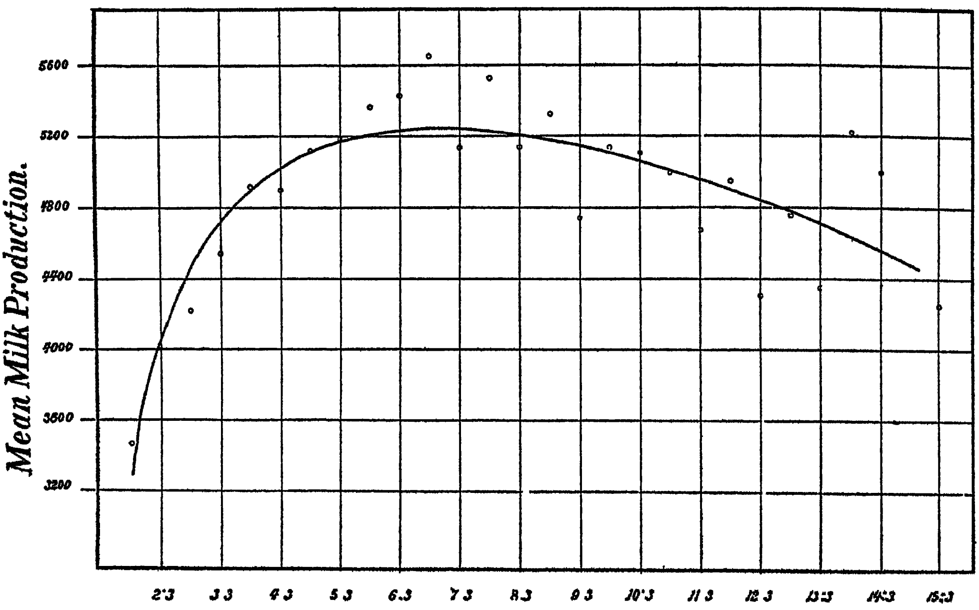

FIG. 1. DIAGRAM SHOWING THE OBSERVED MEANS (SMALL CIRCLES) AND THEORETICAL MEANS FOR JERSEY EIGHT-MONTH MILK PRODUCTION AT ANY GIVEN AGE

The record for the concentration of the

less variation with age. Such being the case, age is not such an important factor in studying the concentration of any given item in milk as it is in studying the quantity of milk. This factor has, however, been taken into consideration, thus eliminating the extraneous influence of age on the concentration of the milk solids.

The general observation that milk yields differ between breeds has indicated that at the foundation many of these differences in producing ability are hereditary. But how and what are the limitations? It is plainly not a simple matter, for if it were, none of our cows would produce less than ten or twelve thousand pounds of milk a year. The problem is not so much to breed animals of higher production than any which we now have as it is to be able to reproduce the best of our present-day stock uniformly and at will. In other words, we wish to know what are the significant facts to be taken into consideration in breeding such stock and what items are of but trivial importance. This problem is made doubly difficult by the fact that it is impossible to measure the character of milk production in the sire. It is, in fact, only possible to arrive at a measure of the influence of the sire on the production of his daughters by indirect means. The first step to be taken towards the better understanding of this problem is, then, to find out the way in which the variations or differences in producing ability behave in their inheritance.

Two general methods of approach have been utilized. The first consists in making carefully controlled crosses between strains whose variation in milk production is known and which do not appreciably overlap in their producing ability. The second consists in studying the variation of production within a given strain of cattle and analyzing the influence of inheritance on this variation. This first method of approach has been utilized by Pearl, Cole, and in a practical sense by Bowlker (see Castle) and Count F. Ahlefeldt-Laurvig (see Ellinger). In a still more limited way the results of Parlour, Stevens, Kildee and McCandlish, Olsen and Biggar, and others, furnish data of some value when considered from this point of view. As the results of these different investigations appear to be alike in their conclusions, it seems necessary to review only the most critical of the work.

The experiment commenced by Pearl, and since 1917 carried on by the writer, consists of controlled matings of three groups of cattle. The first group, the Holstein-Friesian, represents high milk yield and low butterfat percentage; the second group, the Jersey and Guernsey, medium milk yield and high butterfat percentage; the third group, Aberdeen-Angus, low milk yield and a butterfat percentage nearly as high as the Jersey group. Besides these groups, the work also included a few Ayrshire animals with medium milk yield and a butterfat percentage intermediate between the Holstein-Friesian and Aberdeen-Angus. Thus in these classes there are strains of cattle capable of metabolizing large volumes of milk, strains capable of metabolizing medium volumes of milk, and those capable of metabolizing only small volumes of milk. Within these same groups there are strains which regulate this metabolic activity to produce small percentages of butterfat and strains which have high butterfat percentages. When the high milking group is crossed with the medium milking group, the milk yields of the resulting crossbreds are intermediate between the two, approaching most closely those of the high group. When the high milking group is crossed with the low milking group, the resulting crossbreds have milk yields intermediate between

the two, resembling closely that of the medium milking breed. The results appear to be essentially the same whichever way the cross is made. When the medium milk producers are crossed with the low producers, the offspring have milk yields intermediate between the two parental groups. From these results it is clear that it is possible to have an animal extremely heterozygous for its inheritance of milk yield and yet have its yield closely resemble that of a relatively pure strain. Furthermore, since the results are the same either way the cross is made, the experiment indicates the equal influence of both sire and dam on the milk production of the offspring. When the three groups of first generation crossbreds are contrasted it becomes clear, since none of these groups resemble each other or their immediate parents, that the inheritance of milk yield is of the blending type, probably dependent upon a number of factors.

This conclusion is confirmed by the results of the second generation backcrossed progeny. The milk production of these second generation cows shows but little evidence of clean-cut segregation. Production tends to be intermediate between that of the two strains crossed. The evidence thus points to the conclusion that the production of quantity of milk is dependent upon a number of different factors in its inheritance.

The production records of the first generation crossbreds between the high-producing Holstein-Friesian and medium-producing Guernsey group as made in the Bowlker herd have been analyzed by Castle. Thirty-one of these first generation heifers in their first lactation showed milk yields which resembled the Holstein-Friesian parent 1.9 times as closely as they did the Guernsey parent. In the second lactation the milk yield of these crossbred cows was 3.8 times as close to the Holstein-Friesian parent as it was to the Guernsey parent. These results, therefore, support those indicated above.

Ellinger has analyzed the results of the crosses between the Red Danish and Jersey cattle as made in Count Ahlefeldt-Laurvig's herd. Using ten weeks of the first lactation as his measure of the cows' producing ability and cows 28 to 35 months old, the Red Danish animals produced 1,975 pounds of milk, while the Jerseys produced 1,568 pounds of milk. The first generation crossbred animals produced 1,835 pounds of milk. The second generation Red Danish backcrosses produced 1,941 pounds of milk, whereas the second generation Jersey backcrosses produced 1,635 pounds of milk. For the third generation animals resulting from backcrosses of Jerseys onto second generation Jersey backcrosses, or seven-eighths Jerseys, the milk production was 1,543 pounds of milk. These results indicate that the inheritance is of a multiple factor type. The high milk yield shows that there is a tendency for the first generation crossbred's milk production to be increased slightly by heterosis, or that the factors for high milk yield are more dominant than those for low milk production.

BUTTERFAT PERCENTAGE

The influence of inheritance on the butterfat percentage of the crossbred cows for the experiments indicated above is of particular interest in that this influence finds expression in the regulatory processes governing the concentration of the solids in milk rather than those governing its quantity. It will be recalled that the information leads to the hypothesis that the phosphatids are the raw materials from which the butterfat of the milk is made. For Holstein-Friesian cows this butterfat ranges from 2.3 to 4.7 per cent. For Guernsey cattle the butterfat percentage

is much higher, ranging from 3.6 to 7.2 per cent. The butterfat percentage of Jersey cattle ranges from 3.3 to 8.0 per cent. The frequency distribution for Ayrshire cattle is still different, ranging from 2.5 to 6.6 per cent. Since the frequency curves for each breed's butterfat percentage are quite characteristic and distinct from those of the other breeds, it is evident that there is a distinct physiological mechanism by which a cow is able to concentrate butterfat in her milk. Such being the case, it is of interest to examine the results of crosses between these breeds as a means of indicating what part inheritance may play in controlling the cow's ability to concentrate this item of milk secretion.

The experimental matings forming the herd collected by Pearl and Gowen contain crosses of the four breeds, Jersey, Guernsey, Holstein-Friesian, and Ayrshire. The widest differences existed between the butterfat percentages of the Holstein-Friesian and the Channel Islands breeds, Guernsey and Jersey. Smaller differences were found for the Jersey and Ayrshire crosses. The results from these experiments show that the crossbreds from a high butterfat percentage group mated to a low butterfat percentage group have a butterfat percentage intermediate between the two groups but slightly nearer the low butterfat percentage group. The crosses of Ayrshire and Jersey give cattle whose butterfat percentage is also intermediate between the two groups. These results point to the conclusion that butterfat percentage is controlled in inheritance by multiple factors. Since there was no evident difference between those matings in which the sire and those in which the dam came from the high butterfat percentage group, it follows that the sire and dam appear to play an equal rôle in the butterfat percentage of their offspring. The second generation cows thus far obtained from this herd are largely backcrosses of the first generation animals on the purebred parents. These second generation offspring show a fairly wide variation in their butterfat percentages. There is but slight evidence of clean-cut segregation of the single factor type. The results clearly point to the deduction that the concentration of the butterfat in the cow's milk is dependent upon multiple factors.

The butterfat percentages of the crosses between the Holstein-Friesian and Guernsey cattle as made for the Bowlker herd and analyzed by Gaines and Yapp show that for 47 of these first generation heifers the butterfat percentage was intermediate between the two breeds. The variation of this butterfat percentage was rather large. For the second generation animals, the butterfat percentage was about the same as that for the first generation animals and the variation for the group was only slightly greater than that of the first generation. Here again the conclusions to be drawn from these data are the same as those indicated above,—that the sire and dam are equally responsible for the butterfat percentage of the cow and that this butterfat percentage is in large measure dependent upon a number of factors in its inheritance.

Ellinger's analysis of the inheritance of butterfat percentage by crosses between the Red Danish and the Jersey breed may be summarized as follows. The Red Danish breed is much like the Holstein-Friesian in that its butterfat percentage is low. For the cattle used as parents this percentage was 3.56 per cent. The Jerseys used as parents had an average butterfat percentage of 4.94 per cent. The first generation crossbreds were almost intermediate between the two breeds, namely, 4.21 per cent. When the first generation crossbreds were bred back to the Red

Danish breed, the butterfat percentage of these second generation offspring was reduced to 4.04 per cent. When the first generation crossbreds were bred back to the Jersey breed the butterfat percentage was raised toward the Jersey level, the average being 4.53 per cent. For these second generation backcross Jerseys bred back to a Jersey bull, the third generation offspring had a butterfat percentage of 4.60 per cent. These results show clearly the influence of both sire and dam on the butterfat percentage of the progeny. They likewise show that the butterfat percentage of a cow is dependent upon her ancestry, or that butterfat percentage is inherited and inherited in a typical multiple factor manner. These multiple factors may possibly show a slight tendency to dominance of the low butterfat percentage factors or heterosis may be effective in lowering slightly the butterfat percentage of the progeny.

INHERITANCE AS A FACTOR IN THE VARIATION OF THE OTHER MILK CONSTITUENTS

The metabolizing rates of Holstein-Friesian and Guernsey cattle differ with regard to their ability to synthesize the proteins of milk. Yapp has shown that for the milk of the Holstein-Friesians in his herd the protein content was 3.1 per cent, whereas for the milk of the Guernseys the protein content was 3.9. While this difference is not large it appears to be significant. The first generation offspring resulting from the cross of these two breeds have an average protein content of their milk of 3.4 per cent. In other words, the percentage of protein is intermediate between the two parental races. Little or no segregation is shown for the second generation offspring as their protein content was 3.5 per cent. From these results it appears that the animal's ancestry markedly influences the protein content of its milk and that the inheritance factors for this protein content show no clear-cut evidence of segregation.

The proteins of milk are probably synthesized from the amino acids of the blood. The results above quoted indicate that the ability to synthesize these proteins and to determine their concentration in milk is an innate factor within certain breeds. The results further demonstrate that the concentration of the proteins within this milk is an inherited characteristic of the animal wherein the parents play an equal part.

These same crosses are unsatisfactory as material to determine whether or not the lactose content of milk is dependent upon inheritance, for the Holstein-Friesian and Guernsey cattle used in these experiments had essentially the same lactose per cent. Thus the Holstein-Friesian breed's lactose per cent was 4.918 ± 0.041, while the Guernsey's lactose per cent was 5.100 ± 0.023. The lactose percentage in these two breeds must be determined largely by the same factors. The first generation crossbreds' lactose per cent was, however, intermediate between the two breeds, being 5.007. The second generation hybrid was also intermediate between the two breeds, being 4.989 per cent.

The results indicate that the ash of milk is an inherited characteristic similar to that of the other constituents. In the analysis no attempt was made to separate the different elements of the ash. The two breeds, Holstein-Friesian and Guernsey, differ by about 10 per cent in the ash content of their milk. The Holstein percentage is 0.68, whereas the Guernsey milk's content is 0.75 per cent. The first generation is intermediate with a tendency toward the Guernsey, its ash content being 0.73. The second generation is also intermediate between the two types with an ash content of 0.72 per cent.

There is no greater variability in F_1 or F_2 than in the parents, thus indicating that a number of factors are involved in the transmission of this composite character.

INHERITANCE OF MILK YIELD AND BUTTERFAT PERCENTAGE WITHIN PURE BREEDS

The variation of production or butterfat percentage within the pure breeds of cattle furnishes another group of data by which the mechanism controlling this variation may be further elucidated. As indicated above, milk production or butterfat percentage shows much less variation within the so-called "pure breeds" than in crosses made between breeds. The variation, however, is still large. Thus Holstein-Friesian milk production, in its Advanced Registry, varies between 9,000 and 35,000 pounds for the year period. The Guernsey milk production varies between 6,000 and 22,000 pounds for the 365-day period. The Jerseys show a similar range. The range of variation for butterfat percentage is also large for the pure breeds. The Holstein-Friesian butterfat percentage ranges from 2.3 to 4.7; that of the Guernsey and Jersey from about 3.5 to 8.0. The pure breeds plainly offer an excellent opportunity to test the influence of heredity on milk secretion.

The type of data found in the advanced registers of these three breeds necessitates a different analytical mode of approaching these problems from that heretofore utilized. In place of controlling certain variables, it becomes necessary to measure them and determine their effect within the given universe which permeates the data. The correlation method is suited to this purpose when, as in this case, the data conform in their behavior to the assumptions underlying it.

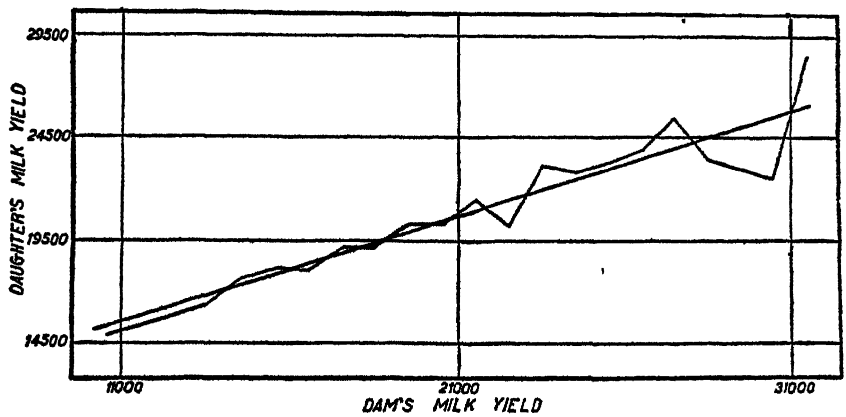

FIG. 2. RELATION BETWEEN THE MATURE-FORM PRODUCTION OF DAUGHTERS AND THEIR DAMS FOR HOLSTEIN-FRIESIAN ADVANCED REGISTRY CATTLE

The relation which exists between the milk productions of daughter and dam furnishes perhaps the most direct test of the effect of inheritance on this character. Figure 2 shows this relation between the milk production of daughters and dams in the Holstein-Friesian breed. The irregular line shows the actual average daughters' milk yields for the given dams' milk yields. The straight line shows the general trend of the data. From this figure it is clear that as the dams' milk productions increase, the daughters' average milk productions also increase. The increase is furthermore at a uniform rate. The

correlation coefficient measuring this relationship is 0.50 ± 0.02. It has been possible to show that this population is nearly random bred. Such being the case, and in view of the multiple factor nature of milk quantity inheritance, it would be expected that the correlation between the dam's production and that of her daughter would be 0.5. Thus the result of actually measuring this relationship checks exactly with that expected from previous knowledge and theory. The relation between the production of daughter and dam in the Guernsey breed is measured by a correlation coefficient of 0.36 ± 0.02. In the Jersey breed the correlation coefficient is 0.30 ± 0.01. These correlation coefficients are somewhat less than would be expected from a random bred population. They agree in showing that a fairly close relation exists between the milk production of parent and offspring in these three breeds. The results for the butterfat concentration which the cow is able to secrete in her milk are essentially similar to those for milk yield. The correlation coefficient between daughter and dam for the Holstein-Friesian is 0.41 ± 0.02, for the Guernsey 0.42 ± 0.02, and for the Jerseys 0.42 ± 0.01. The results for the butterfat percentage of the three breeds agree closely in showing that the level of the daughter's butterfat percentage is partially determined by that of her dam. They are furthermore in practical agreement with the hypothesis that the previous results have indicated, namely, the inheritance of butterfat percentage through multiple factors. It is thus shown that the inheritance of milk yield and butterfat percentage is of the same type. It remains to be shown whether or not they take place by the same factors or by different ones.

In the Holstein-Friesian breed, where there is no physiological correlation between milk yield and butterfat percentage found in the cow's milk, it is possible to approach this problem by comparing the butterfat percentages of the dam with the milk yields of the daughter; for if the same factors are responsible for determining the inheritance of both variables, then a comparison of one variable in the dam with the other in the daughter should give correlation coefficients which are of the same magnitude as those derived from a comparison of the same variable in each, whereas if the inheritance is by separate factors, little or no correlation would exist between the one record in the parent and the other record in the daughter. For the Holstein-Friesian cows there is no correlation between the milk yield of the daughter and the butterfat percentage of the dam, or the butterfat percentage of the daughter and the milk yield of the dam. These results therefore establish the conclusion that milk yield is inherited through a separate set of factors from those for the inheritance of butterfat percentage.

The amount of influence of the sire upon the production of his daughters may be determined from the fact that for any given sire the records of his daughters will all fall in one array of the correlation table. The variation of those records in relation to those of the whole population makes it possible to calculate the correlation coefficient between the production of the daughter and that of the sire, even though it is impossible to measure the sire's production. When this calculation is completed, the Holstein-Friesian sire has a correlation coefficient between the daughter and his potential record of 0.52 for milk yield; that for the Guernsey sire is 0.50. The correlation coefficients for the butterfat percentage of sire and daughter are,—for the Holstein-Friesian breed 0.53 and for the Guernsey breed

0.54. These correlation coefficients agree within practical limits with those found in the same breeds for the relation of production of daughters and dams. The sire is, therefore, equally important with the dam in determining their offspring's milk production or butterfat percentage, even though this potential inheritance is never physiologically expressed by the male.

This conclusion may be checked in another manner. Full sisters have a common sire and a common dam, half sisters have either the sire or dam in common but not both. If the sire alone or in major part determines the production of his daughter, the above relationships would lead to the expectation that full sisters would resemble each other in their production and half sisters with a common sire would resemble each other in their production to the same or nearly the same degree that full sisters are correlated. Half sisters with a common dam would not resemble each other or would resemble each other only to a slight degree. If, on the other hand, both the sire and dam determine the production of their daughters to the same or nearly the same extent, the full sisters' production would be fairly closely correlated. The half sisters' production would be correlated but to a less degree than the full sisters', and further, the correlation coefficients between the half sisters should be of the same order of magnitude. If, as a last alternative the dam determines the production, the expected relation would be,—the full sisters' production correlated; the half sisters' production, where the sire is the common parent, not correlated; half sisters with a common dam correlated in their production to the same degree as full sisters. The actual results show that full sisters resemble each other more closely in their milk yields and butterfat percentages than half sisters for the three breeds, Holstein-Friesian, Guernsey, and Jersey. The full sisters are correlated in their milk yields as follows: Holstein-Friesian, 0.55 ± 0.03; Guernsey, 0.41 ± 0.02; Jersey, 0.39 ± 0.02. Half sisters with a common sire have the following relations between their milk yields: Holstein-Friesian, 0.36 ± 0.02; Guernsey, 0.13 ± 0.02; Jersey, 0.23 ± 0.01. The milk yields of half sisters with a common dam show the following correlations: Holstein-Friesian, 0.38 ± 0.03; Guernsey, 0.15 ± 0.02; Jersey, 0.20 ± 0.01. The results for the inheritance of butterfat percentage are of similar order of magnitude,—full sisters: Holstein-Friesian, 0.46 ± 0.03; Guernsey, 0.44 ± 0.02; Jersey, 0.41 ± 0.01. Half sisters with a common sire show the following relations: Holstein-Friesian, 0.37± 0.02; Guernsey, 0.17 ± 0.01; Jersey, 0.25± 0.01. Half sisters from a common dam are correlated thus: Holstein-Friesian, 0.22 ± 0.04; Guernsey, 0.19 ± 0.01; Jersey, 0.20 ± 0.01. Full sisters resemble each other more closely in their milk yields and butterfat percentages than half sisters. The half sisters from a common sire or from a common dam have practically the same degree of resemblance. The hypothesis that the sire and dam are equally and jointly responsible for the milk productions and butterfat percentages of their offspring is consequently borne out by this comparison. The results are furthermore in accord with the expectation of a random-bred Mendelian population. For such a population the relation between full sisters should be measured by a correlation coefficient of 0.5, for half sisters by a correlation coefficient of 0.25. Actually for the three breeds averaged together the correlation coefficient for the milk yields of full sisters was 0.45 and that for half sisters 0.24. For butterfat percentage the correlation

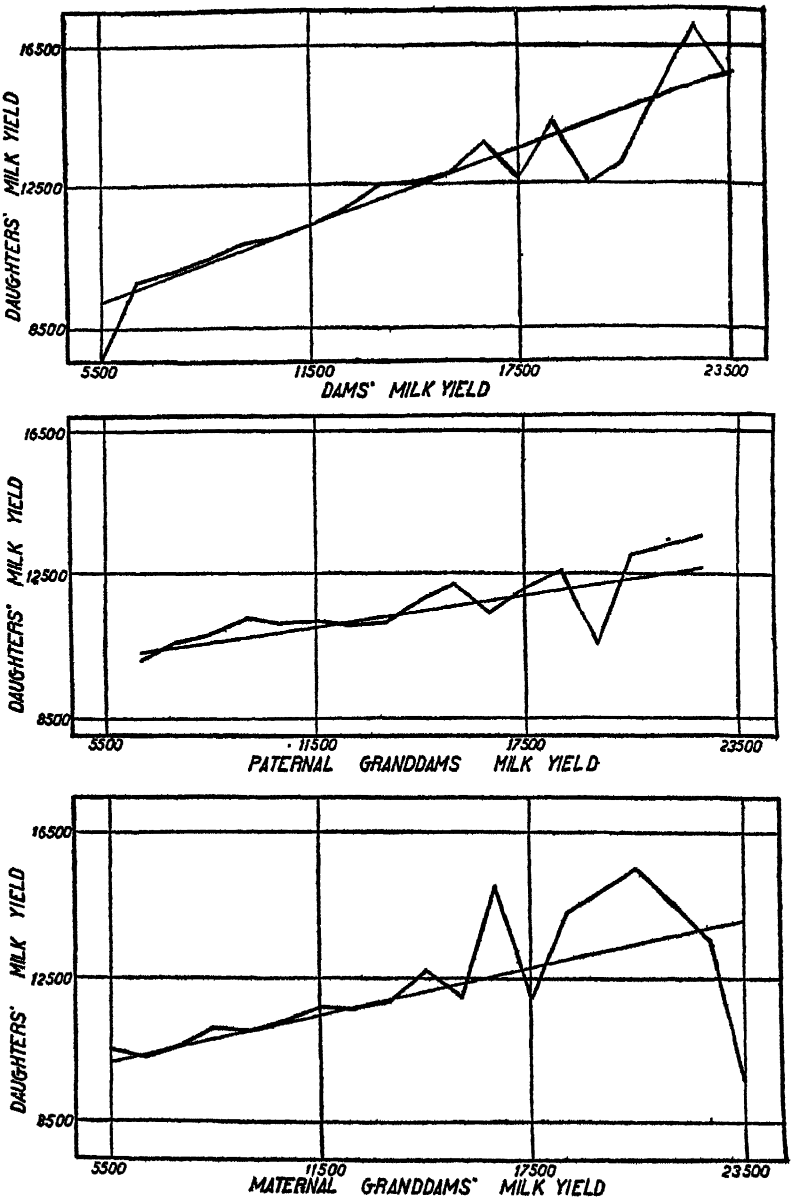

FIG. 3. AVERAGE MILK YIELDS OF DAUGHTERS OR GRANDDAUGHTERS FOR DAMS OR GRANDDAMS IN THE GUERNSEY ADVANCED REGISTRY

The upper graph shows the relation between the daughter and dam. The middle graph the relation between granddaughter and paternal granddam. The lower graph the relation between the granddaughter and maternal granddam. Examination of these graphs shows that for either type of ancestors an increase in the milk production results in an increased average production of their daughters or granddaughters. Contrasting the average production of the daughters for an increase in the production of the dams as compared with an average production of the daughters for a like increase in the production of the granddam, it is found that a given increase in the dam's production results in a much more marked average increase in the daughter's production, in fact nearly twice as great an increase in production as that found for granddam and granddaughter.

coefficient was 0.43 for full sisters and 0.23 for half sisters.

It is of interest to note that on an inheritance view, the ancestors further removed than one generation should play a prominent part in the control of the secretory activities of the mammary glands. The interrelation between the production of daughter, dam, and granddam is shown in figure 3. The upper chart shows the relation between the daughter and dam. The middle chart the relation between the granddaughter and paternal granddam. The lower chart the relation between the granddaughter and maternal granddam. Examination of these charts shows that for either type of ancestors an increase in their milk production results in an increase in the average productions of the daughters or granddaughters. Comparison of the average production of the daughters for a given increase of production in the dam with the average production of the daughter for a like increase in the production of the granddam shows that an increase in the dam's production results in a much more marked increase in the daughter's production, in fact twice as great an increase in production as that caused by the granddam. This conclusion is supported by the three breeds, Holstein-Friesian, Guernsey, and Jersey. It is true for both the yield of milk and for the butterfat percentage in the milk. The different grandparents, paternal and maternal are about equally important. In terms of correlation these relations for granddaughters' and granddams' records are,—for milk yield: paternal granddam, Holstein-Friesian, 0.26 ± 0.04; Guernsey, 0.16 ± 0.01; Jersey, 0.20 ± 0.01; for the maternal granddam, Holstein-Friesian, 0.31 ± 0.05; Guernsey, 0.20 ± 0.02; Jersey, 0.14 ± 0.02. Comparing these results with those obtained for the relation between the daughter and dam, the grandparents have about half the correlation with the daughter's production that the dam has. Similar results are obtained from the butterfat percentage. For Holstein-Friesian, Guernsey, and Jersey breeds, the paternal granddams are correlated with their granddaughters' productions to the following extent: 0.09 ± 0.04, 0.15 ± 0.01, 0.21 ± 0.01. The maternal granddams are correlated with their granddaughters' productions as follows: Holstein-Friesian, 0.19 ± 0.05; Guernsey, 0.20 ± 0.02; Jersey, 0.25 ± 0.02. The average correlation for the butterfat content of the milk of the granddams and granddaughters for the three breeds is 0.18, or the granddaughters' butterfat percentages are correlated with their granddams' butterfat percentages to about half the magnitude that they are correlated to their dams'. The mechanistic control of milk production and butterfat content, as organized within the cow, is thus in part portrayed by the performance of both the parents and grandparents.

Another ancestral combination used in dairy cattle breeding is that of cousins. The importance of this combination comes from the habit of giving a good deal of weight to the production records of the brother's daughters in selecting a bull for a herd sire. The daughters of such a bull would, of course, be cousins to the daughters of his brother. The study of this relation for both yield of milk and the butterfat percentage it contains for the Holstein-Friesian breed shows that there is a small degree of relation between the production record of one cousin and that of another. For milk yield the average relationship on the correlation scale is 0.15, for butterfat percentage the average relationship is 0.16. The quantitative

relations agree fairly well with those demanded by the Mendelian theory of inheritance through multiple factors.

A similar combination of ancestors by which further evidence for the Mendelian theory of milk production may be adduced is that of the relation between the productions of aunt and niece. This combination is used sometimes in selecting a herd bull, because of the belief that his daughters will duplicate the milk productions of his sisters. The relationship between a sire's daughters and his sons' daughters is that of aunt and niece. In making this comparison the average production of the aunt was contrasted with the average production of the nieces. The correlation coefficients measuring this relationship are,—for the milk yields of Guernsey cattle, 0.26 ± 0.02; and for butterfat percentages, 0.18 ± 0.02. These correlation coefficients agree with those expected in a Mendelian population, breeding at random and involving multiple factors.

The known facts regarding the variations of milk production may now be examined from a somewhat different viewpoint. The milk production of a cow varies from lactation to lactation. Contrasted with the other cows of the herd, the cow under consideration may in a given year be the highest producer of milk and in the following year drop in production to be the tenth highest producer in, say, a herd of fifty cows. The question may be asked what are the factors which bring about the degree of permanence of a cow's position in a given herd with respect to her milk production, for such a case as that illustrated above. A little consideration of this question shows that this permanence must be accounted for by influences which have preceded the time of milk production. The cow's heredity and environment before the lactation would be the important factors tending to stabilize the cow's production to a given level. The unstable factors would be those of environment and climatic conditions and changes of food tending to cause variation within the given lactation. In the earlier results here reported, the influence of heredity is measured. It is possible, therefore, to contrast this influence in determining the permanence of a cow's production with that found to exist in the permanence of production from one lactation to another.

For the Holstein-Friesian breed the average correlations between the records of one lactation and those of another are found to be 0.667 for milk yield and 0.715 for butterfat percentage. These correlations measure the cow's permanence in the production of milk and butterfat percentage. They measure the influence of those factors of environment which tend to cause a permanent difference in quantity or quality of milk, combined with the effect of those for heredity. The effect of the dam's contribution to the heredity of the daughter for milk yield is indicated by the correlation coefficient 0.50. The influence of the sire's contribution to the daughter's milk production is 0.52 as measured on the correlation scale. It is not possible to obtain the correlation between the sire's and dam's performance. The next best measures of this cross correlation, or the degree of assortative mating, are those between the paternal granddam's record and the record of the cow to which her son is bred, correlation 0.14, and between the two granddams' records, correlation 0.30. It will be noted that these cross correlations decrease as the animals compared approach the cow under consideration. It is therefore reasonable to suppose that the correlation of sire and dam is not more than 0.14, and probably less than this figure. From these data the total

influence of the two parents' heredity on the daughter's performance in milk yield is 0.67. The multiple correlation for the parents' and grandparents' records with the daughter's milk production is 0.68. These correlations are numerically identical in value with that measuring the degree of permanence in a cow's milk yield, 0.667. It is thus evident that it is the inheritance a cow receives which tends to make her milk production at a permanent level when contrasted with that of other cows.

The data for the butterfat percentage may be treated in the same manner. The average parental correlation for sire and dam with the daughter's butterfat percentage is 0.47; the average grandparental correlation is 0.25. The correlation for assortative mating as indicated by the relation of the butterfat percentages of paternal granddam and dam is 0.001; for the maternal grandparent's butterfat percentage it is 0.04. In other words, it is justifiable to assert that there is no true selective breeding for butterfat percentage within the breed. With these data the multiple correlation of the parents' and grandparents' butterfat percentages with the butterfat percentage of the daughter is found to be 0.67. For the parents alone the multiple correlation was 0.67. The correlation between the butterfat percentage of one lactation and that of another is 0.72. This correlation, like that for milk yield, can be interpreted as due to the influence of constant environmental conditions or heredity. The multiple correlation of the parents' and grandparents' records with that of the daughter shows that practically all of the permanence in the cow's ability to secrete butterfat percentage is due to the influence of inheritance.

SUMMARY

In this review an attempt has been made to portray the interaction of recognized biological factors leading to milk production. Milk itself is a product of great metabolic activity on the part of the mammary gland. Some of the raw materials for its synthesis are apparently dextrose, phosphatids, and amino acids, the dextrose being converted into lactose, the phosphatids into fat, and the amino acids into proteins. Individual animals vary greatly in their ability to synthesize these products and form quantities of milk or to regulate the concentration of the different constituents in the milk. When the causes of this variation are examined heredity in its broad sense is found to be the primal cause of this variation. Thus the parents or grandparents may to a large degree portray the relative milk yield or concentration of the milk solids of a given cow as contrasted with other cows. It was further shown that the relative amount of milk which was secreted and the butterfat content of the same were independent in their inheritance for Holstein-Friesian cattle. Finally the cow and her relatives were shown to be correlated in their milk productions, etc., as would be expected for Mendelian inheritance in its most generalized case, multiple factors and random mating.

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THE GROWTH OF POPULATIONS

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VARIABLES

THE primary biological variables involved in the growth of population are two in number: the force of *natality*, measured by the birth rate, on the one hand; and the force of *mortality*, measured by the death rate, on the other hand. These primary elements are fundamental to the discussion of the growth of populations of any and all organisms whatever, from *Amoeba* to man. In most of the lower organisms living in a state of nature, whether plant or animal, these are the only first-order variables which have to be taken into account in discussing the problem, and in experimental studies on population growth the arrangement of the experiments is usually such that only natality and mortality can possibly directly determine the number of individuals in the population at any given time.

In most human populations, especially those inhabiting large geographical areas, a third factor may influence directly the size of the population at any given moment, in greater or less degree. This third factor is *migration*, and it is theoretically to be regarded as a primary variable in determining the growth of such human populations.

Besides the three primary biological factors of natality, mortality, and migration which influence the observed growth of human populations there are various secondary environmental factors which may play a part in determining the final result. These are such things as food supply, the economic situation in general and in particular, social forces of various sorts, and perhaps others. But it should always be kept in mind, and this I particularly wish to emphasize, that these are all *secondary* factors from a biological point of view. They produce whatever effect they may have upon the final result, namely the size of the population at any given moment, by acting, more or less powerfully as the case may be, upon one or more of the three primary biological variables, natality, mortality, and migration. Thus an economic depression in a particular country may affect adversely the birth rate of that country, or even the death rate if the degree of the depression is sufficiently great or its duration sufficiently prolonged. These effects will, in greater or smaller degree, reflect themselves finally in the size of the population. This final effect upon the growth of the population may, however, be extremely slight, and difficult or even impossible of separate statistical recognition or measurement, because of compensating influences at work at the same time. Logically, however, the operation of these secondary factors must always be recognized. But from the point of view of the theory of population growth their influence is always a second order one. They can produce any effects upon population only by operating upon the primary biological forces of natality, mortality, and migration.

HOW POPULATIONS GROW

It is an observed fact, which at this stage of the discussion involves no theoretical implications whatever, or postulates special to it, that the growth of populations of the most diverse organisms follows a regular and characteristic course. In general and everyday terms of common sense this characteristic manner of population growth may be described in the following way. The population at first grows slowly, but gains impetus as it grows, passing gradually into a stage of rapid growth, which finally reaches a maximum of rapidity. After this stage of most rapid growth the population increases ever more and more slowly, until finally there is no more perceptible growth at all. In short, the populations of various forms of life first wax in their speed of growing and then wane.

This characteristic phenomenon may be more precisely described in a variety of ways, depending upon which of several mathematical aspects of the matter we choose to stress. This may best be illustrated by a concrete example. For this we may well take a relatively simple case biologically, such as is afforded by the growth of a population of yeast cells. The yeast plant is an organism low in the scale of life. Its reproduction, under the conditions of the experiments, is by the process of cell division, the cells present at any given moment forming new cells by budding. An experiment on the growth of a population of yeast cells is made as follows: A measured amount of wort, which furnishes nutriment to the yeast plants, is seeded with a few cells. Then at equal intervals of time thereafter the equivalent of a census count is made of the cells then present. Because of the minute size of the individual cells, and of other technical difficulties, some sort of indirect method is commonly used to measure the size of the population, in place of direct counts. But this is a matter merely of detail, which need not detain us in the present discussion.

The outcome of a typical experiment of this sort, the data being taken from an

TABLE 1

Growth of a population of yeast cells (data from Carlson)

HOURS OF GROWTH	QUANTITY OF YEAST		ABSOLUTE QUANTITY OF YEAST PRODUCED PER HOUR (= TIME RATE OF GROWTH)	QUANTITY OF YEAST PRODUCED PER HOUR IN PER-CENT OF TOTAL UP TO THAT HOUR (= PER-CENTAGE RATE OF GROWTH)
	OBSERVED	CALCULATED		
(*a*)	(*b*)	(*c*)	(*d*)	(*e*)
				per cent
0	9.6	9.9	8.7	90.6
1	18.3	16.8	10.7	58.5
2	29.0	28.2	18.2	62.8
3	47.2	46.7	23.9	50.6
4	71.1	76.0	48.0	67.5
5	119.1	120.1	55.5	46.6
6	174.6	181.9	82.7	47.4
7	257.3	260.3	93.4	36.3
8	350.7	348.2	90.3	25.7
9	441.0	433.9	72.3	16.4
10	513.3	506.9	46.4	9.0
11	559.7	562.3	35.1	6.3
12	594.8	600.8	34.6	5.8
13	629.4	625.8	11.4	1.8
14	640.8	641.5	10.3	1.6
15	651.1	651.0	4.8	0.7
16	655.9	656.7	3.7	0.6
17	659.6	660.1	2.2	0.3
18	661.8	662.1		

investigation of the subject made by Carlson (3), is shown in table 1. A further discussion of these data will be found in an earlier work (8). The figures of columns (*b*) and (*c*) are shown graphically in figure 1.

In table 1 the first column (*a*) gives the hours during which growth occurred; the second column (*b*) records the observed quantity of yeast, or in other words the size of the population, at each successive

hour; the third column (*c*), which may be neglected for the present, gives the size of the population at each successive hour as calculated from a mathematical equation to be discussed later; column (*d*) gives the simple time rate of growth, that is the absolute amount of new yeast produced by the growth of the population in each successive hour. The figures in this column are the observed values of the

Column (*d*) tells us that in the growth of this yeast population the absolute increment of new yeast cells per unit of time *increases* each hour as the population grows, up to a maximum increment per hour, which is attained in this case somewhere about the 7th or 8th hour. Thereafter as growth continues the absolute increment of new cells per unit of time *decreases* hour by hour until it almost

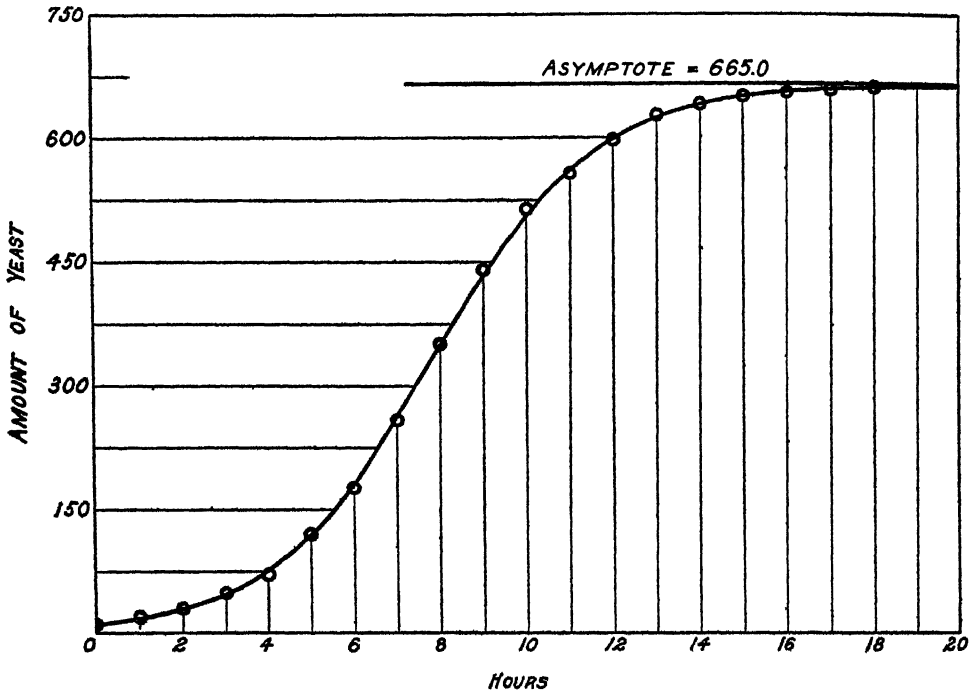

FIG. 1. THE GROWTH OF A POPULATION OF YEAST CELLS

In the publication of this diagram in (8), through an error in proof-reading the abscissal units were stated to be days, when they should have been hours, as is correctly shown here. (Data from Carlson.)

ratio dy/dt, y denoting the size of population and t denoting time in hours. The last column (*e*) gives the relative rate of growth, in proportion to the already attained size of the population, in each time interval. In mathematical terminology the figures in this column are the observed values of the double ratio $\frac{1}{y} \cdot \frac{dy}{dt}$ for each hour.

vanishes, and, for all practical purposes, the population has ceased to grow.

If the figures of column (*d*) are plotted, as in figure 2, they obviously form a curve shaped like a cocked hat or sugarloaf, low at the two ends and rising to a peak near the middle. As a natural consequence of this trend of the first differences the relative growth rates given in column (*e*) are found to be largest at the

start of growth and to become smaller as the absolute size of the population increases. Although this relative rate of growth presented in column (*e*) is the one most often discussed by demographers in talking about population growth, it tells us much less clearly what is the real nature of the characteristic curve of such growth than does the simple time rate, or first derivative of the population growth curve given in column (*d*).

recent books (6, 8). It has been shown that experimental populations of yeast, of bacteria, and of the fly *Drosophila melanogaster*, in their growth follow this characteristic curve with great precision.

Furthermore it has been demonstrated statistically that populations of human beings have grown according to the same type of curve, so far as may be judged from the available census records, in at least the following countries: Sweden,

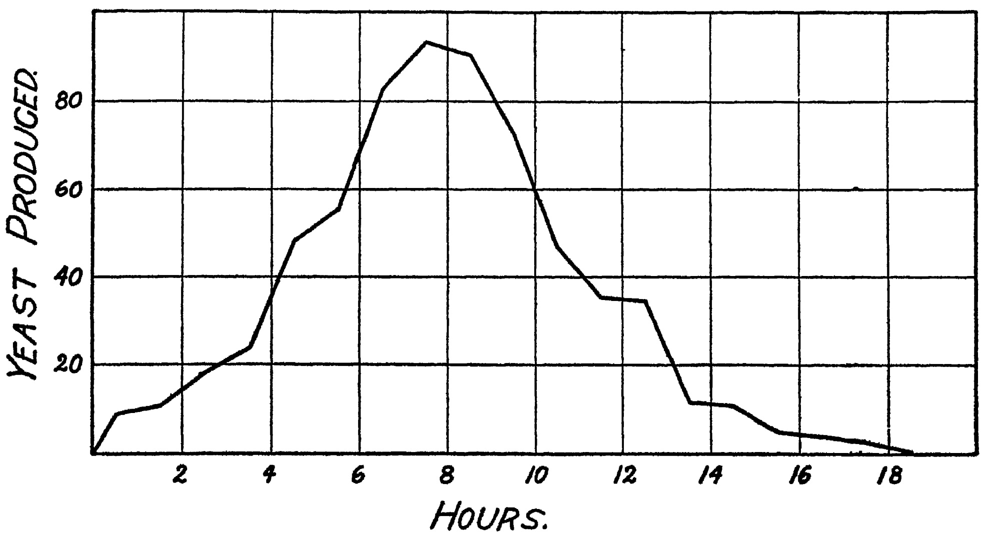

FIG. 2. GROWTH INCREMENTS OF YEAST POPULATION IN SUCCESSIVE TIME INTERVALS
Data from column (*d*) of table 1

The phenomenon shown in column (*d*), namely that the absolute increment of growth per unit of time increases with time to a maximum value, and then decreases till the end of measurable growth is reached, has been found in recent years to be the way in which populations of such a wide variety of organisms actually grow, that it may now be fairly regarded as the characteristic, normal mode of population growth, to at least a first approximation. I shall not take the time here to review all the evidence that this is so. This has already been done in two

United States of America, France, Austria, Belgium, Denmark, England and Wales, Hungary, Italy, Norway, Scotland, Servia, Japan, Java, Philippine Islands, Baltimore City, New York City, and the world as a whole.

In illustration of this statement four cases are presented graphically here. These are the United States (fig. 3), Sweden (fig. 4), France (fig. 5), and the world as a whole (fig. 6). In these diagrams the circles give the census counts (or, in the case of the world as a whole, estimates) of the populations existing at

the given dates, while the smooth curves are the fitted theoretical curves of population growth.

In the case of the demographic units listed above the census records do not

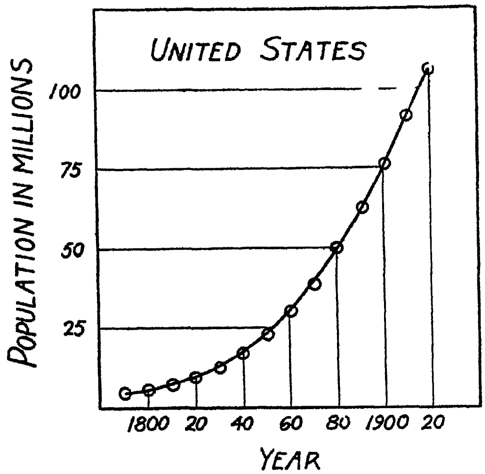

FIG. 3. THE OBSERVED AND CALCULATED GROWTH OF THE POPULATION OF THE UNITED STATES

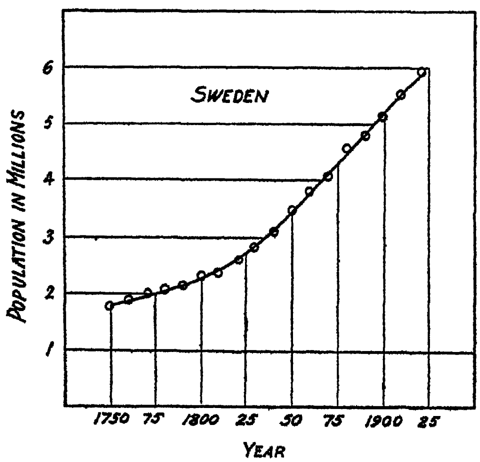

FIG. 4. THE OBSERVED AND CALCULATED GROWTH OF THE POPULATION OF SWEDEN

extend over a sufficiently long time to make the case conclusive that population growth, if undisturbed, would follow in human groups the complete course exhibited by the yeast population just discussed. The available data only make such a conclusion in some degree probable. And one cannot conduct experiments with human beings on this point, as can be done with lower organisms. But fortunately it has been possible to find one group of human beings, the indigenous native population of Algeria, in which a

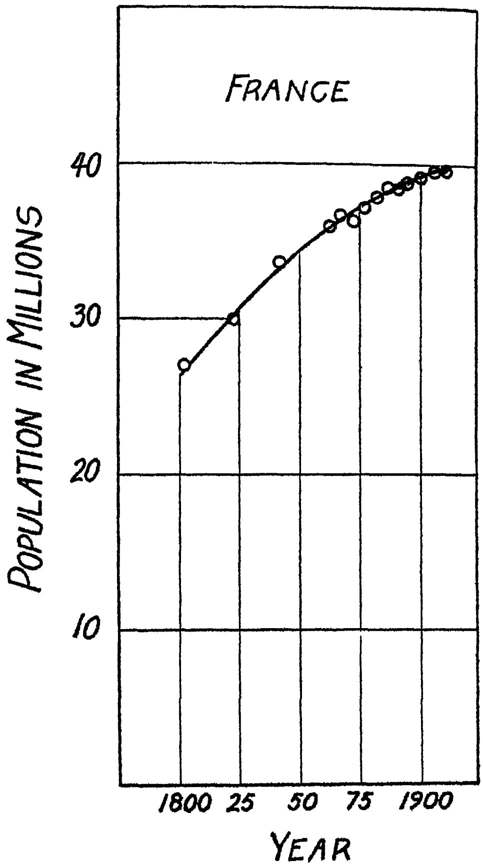

FIG. 5. THE OBSERVED AND CALCULATED GROWTH OF THE POPULATION OF FRANCE

cycle of population growth has been practically completed during the period for which census records are available, these having been carefully made by the French. In this case the human population followed in its whole cycle of growth a curve of the same characteristic form that has been discussed for the yeast. This case has been fully described and

analyzed in my book *The Biology of Population Growth* (8), and is illustrated here in figure 7.

THE LOGISTIC CURVE

The equation to the curve which has been found by experiment and observation to be descriptive of population growth in a wide variety of organisms was first discovered by the Belgian mathematician, Verhulst (18, see also 19, 20) in 1838. His pioneer work was forgotten, and consequently overlooked by most subsequent students of the population problem. In 1920 the present writer and his colleague, Lowell J. Reed, without any knowledge of Verhulst's prior work, independently hit upon the same equation (12).

Verhulst called his curve the "logistic." This usage we shall follow. The characteristic appearance, and some of the mathematical properties of the logistic curve, are shown in figure 8.

The third column of table 1 (column *c*) shows the degree of accuracy with which this logistic curve is able to describe the observed growth of a population of yeast cells. For the whole series of 19 observations the root mean square deviation between the experimental results and the theoretical curve is only 3.59. The equation of the fitted curve is:

$$y = \frac{66.5}{1 + e^{4.1896 - 0.5355x}}$$

where y = quantity of yeast, and x = time of growth in hours.

The possession of such a curve as this, which is found by actual experience to describe accurately the course of population growth in a wide variety of organisms, is a valuable first step, but only a first step, towards reaching an understanding of the biology of the process. What we want to know is how the biological forces of natality and mortality are so integrated and correlated in their action as to lead to a final result in size of population which follows this particular curve rather than some other one. This demands that we shall push the enquiry further.

MATHEMATICAL CONSIDERATIONS

There are two lines along which this further investigation must proceed. The first is a theoretical mathematical analysis of the relation of birth rates and death rates to the logistic curve, under various postulates. We have done a considerable amount of work, as yet unpublished, upon this subject. Certain aspects of it have also been discussed by Yule (25) and Lotka (5). I shall not attempt to present the details of this analysis on this occasion, because of their technical character. Some of the results, however, may be stated in simple form and are pertinent to the present discussion.

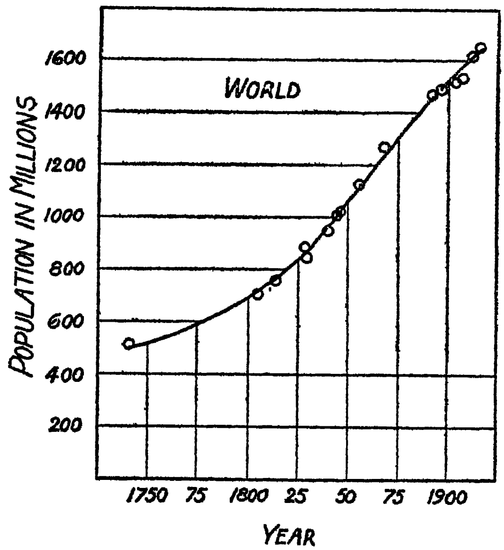

FIG. 6. THE OBSERVED AND CALCULATED GROWTH OF THE POPULATION OF THE WORLD

It is easily shown that if birth rates and death rates are assumed to remain constant, at any values consistent with growth at all (i.e., birth rates larger than

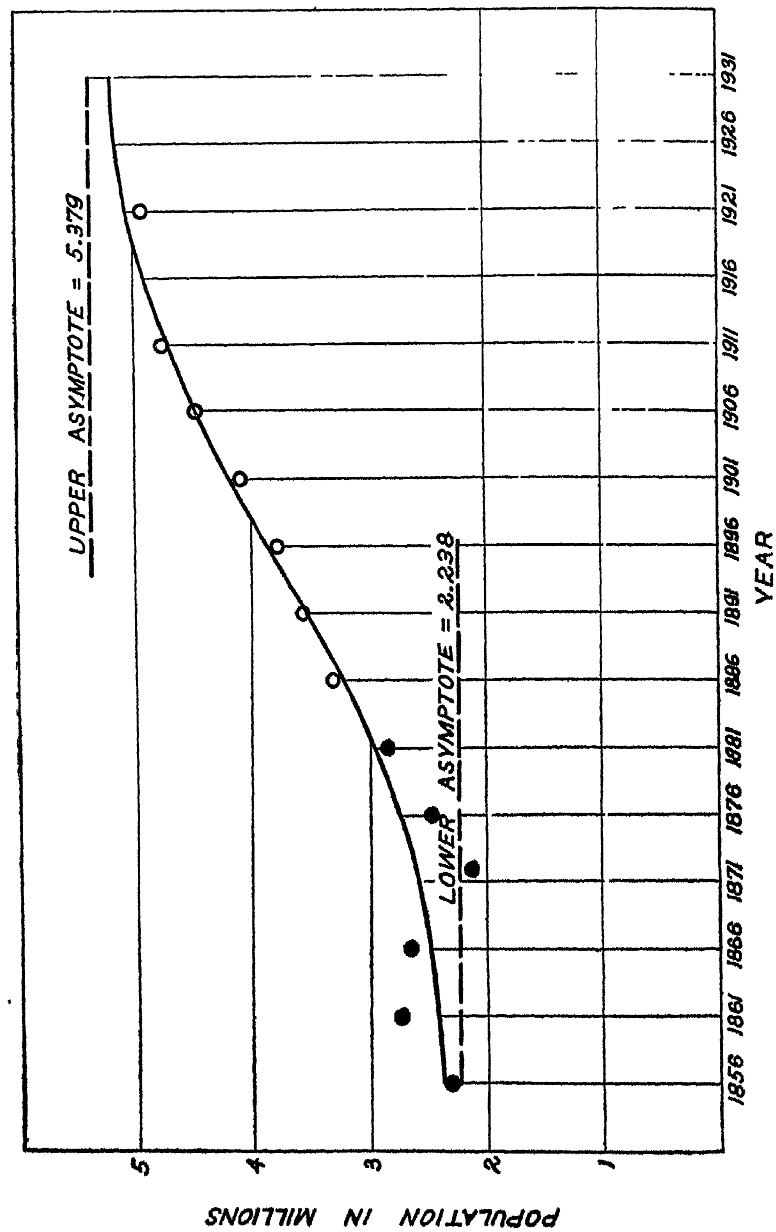

Fig. 7. Observed and Calculated Growth of the Indigenous Native Population of Algeria

death rates) the population will grow according to an exponential curve, on to infinity. The rate of this progression may be slow or rapid according to the assumptions made, but the form is exponential. Nothing like the slowing down of growth after a period, which is seen in the logistic curve, appears under this postulate.

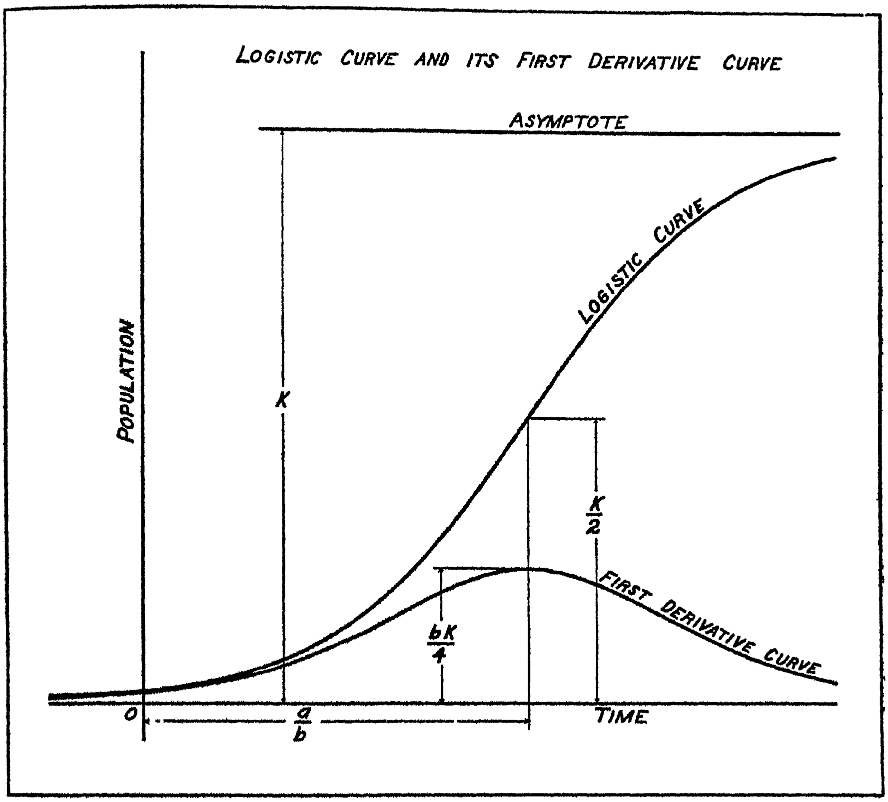

FIG. 8. THE LOGISTIC CURVE AND ITS FIRST DERIVATIVE

But plainly, with actual populations of living organisms, birth rates cannot continue constant indefinitely. In saying that birth rates shall be constant regardless of the size of the population already attained, it is tacitly, but implicitly, assumed that the universe in which the hypothetical population is growing expands proportionately with this growth, so that each single element always has plenty of room, no matter how large the whole group becomes. But such an assumption is unwarranted for any actual population whatever. All populations of real organisms live in universes with definite limits. The absolute size of the universe may be small, as in the case of the test-tube which holds the yeast cells, or it may be as large as the earth, most of which could conceivably be inhabited, on a pinch, by man. But in any and every case there is ultimately a definite limit to the size of the universe in which any real population lives.

This consideration obviously alters the

complexion of the case. For it at once follows that if the universes in which populations live are finite and inextensible, there must come a time in the growth of any population when the individuals composing it begin to get crowded, and as the growth continues beyond this point they will get more and more crowded.

It is not an unreasonable hypothesis *a priori*, and as we shall presently see there is abundant experimental and observational support for the view, that crowding, or as it is technically termed, density of population, when it reaches a certain degree, has an adverse effect upon both of the two primary biological forces underlying population growth, natality and mortality. This assumption has been made and the theoretical consequences worked out, under several simple postulates as to the quantitative relationships between the variables.

The net result of this first, or mathematical, attack upon the problem of population growth is to show that, with simple postulates as to the relations between the two first-order variables, birth rate and death rate, and the second-order variable density of population, and without consideration of any other variables whatever, we are led rigorously to the conclusion that under these postulates the growth of population must necessarily follow that type of curve (the logistic) which is empirically found to describe the growth of actual populations of widely diverse organisms.

EXPERIMENTAL POPULATIONS

The second mode of attack upon the problem of the biology of population growth is the experimental. Its purpose is to observe at each stage the growth of the population of some actual organisms, small enough to be capable of laboratory management, under carefully controlled and known conditions. Not only can the growth of such an experimental population as a whole be observed, but also it is possible to set up experiments in which each separate variable such as natality, mortality, density of population, etc., can be particularly studied, and its behavior under controlled conditions described and measured. It is to this mode of attack upon the problem that much of the research energy of my laboratory has been devoted during the past five years. The organism chiefly used has been the fruit-fly *Drosophila melanogaster*, the form so widely employed as material for genetic studies.

Before undertaking to present some account of the results of these experiments I wish to point out that the significance of these, or any similar experiments on lower organisms, in the discussion of the problem of human populations should be neither over-rated nor under-rated. Obviously in all such experiments the conditions of life are not only simpler but also more uniform than any under which human populations live. Further the organisms concerned are less complex physiologically and psychologically than are human beings. No conclusion reached by the study of experimental populations of lower organisms can safely be transferred by simple inference to human populations. It must in every case be conclusively shown by independent investigation of human populations that the same conclusion holds for them, if it does. Furthermore if the same result is, in fact, found to appear in both experimental and human populations, by no means may it safely be inferred that the causes leading to this result are necessarily the same in the two cases. They may be or they may not. To find out which alternative is true demands special *ad hoc* investigation.

On the other hand it must also be kept

in mind that the forces of natality and mortality are basic biological attributes of aggregates of living things, men as well as flies. The ultimate biological forces leading to the observed growth of a human population are these two, natality and mortality, just as truly as they are in a population of flies or yeast cells. Because of the much greater ease and precision with which the behavior of these variables, under diverse controlled conditions, may be analyzed in experimental populations of lower organisms, the results obtained from such studies may be of great value in the direction of suggesting points for statistical investigation in human populations. Over and beyond this consideration is the further one that populations of whatever organisms are, in their very nature, aggregate wholes, and behave in growth and other ways as such (cf. Wheeler, 21–24). The elements of their behavior arising out of this condition of aggregate wholeness are just as true in populations composed of individuals of one species as in those composed of individuals of another.

Perhaps the most impressive thing which has come out of the statistical study of human population growth is the evidence that the steady onward march of this growth is not sensibly altered from the logistic course, in the great majority of actual cases, by the host of economic and social events which are supposed of logical necessity to affect it. This statement should not be taken to mean that economic and social factors are unimportant in their relation to population growth. So far am I from holding any such opinion that it is my belief that economic forces are probably the most important single element in the biologically effective environment of civilized man today. All that is meant is that, in the majority of observed cases at least, the effect of these factors on human population growth *has in the past, at any rate, been such as to make the growth of the population follow the logistic curve, rather than deviate from it.* During the past few years the argument has been made that the very populations which have in fact grown with great precision according to a logistic curve, cannot possibly have done so, because this curve does not "take account of" a lot of these second-order variables. This argument is rubbish, born out of the conservative resistance to any new idea which the established order of learning has always shown, by that wind-broken and spavined old stallion, faith in *a priori* logic as against plain facts of experience. As a matter of fact the logistic curve does "take account of" all these second- and third-order variables, in the sense that it describes the integrated end effect upon population size of the aggregated forces tending towards increase in numbers on the one hand, and decrease in numbers on the other hand. The population growth of the United States is an excellent case in point. If one plots the census counts of this population from 1790 to 1920 it is impossible to detect in the curve of growth any separate or disturbing effect of immigration, although, as we have seen, migration is theoretically a first-order variable in population growth. The actual observed growth of the population of the United States follows the logistic curve with remarkable precision. To suit various theorists it presumably ought not to, but *in fact* it does. Benjamin Franklin long ago pointed out that for the growth of population aggregates of any considerable size migration was an unimportant factor, as compared with natural increase by reproduction. He was right. Whatever the future may develop, the past history of the matter shows plainly that human populations

have behaved in their growth in the same way that experimental populations of lower organisms do, with truly remarkable faithfulness.

DROSOPHILA POPULATIONS

The details of the technique of making experiments on population with the fly *Drosophila melanogaster* have already been described (8), and need not be repeated here. It will suffice to say that in bottles of measured size definite amounts of food material are placed, and then an initial group of a few flies—say one male and one female—is added. At regular intervals thereafter the then existing population in each bottle is carefully counted and recorded, and the individuals composing it returned to the bottle to carry on their normal lives until the next census count.

TABLE 2

The growth and decline of a hypothetical population assumed to start with two individuals and to be subject thereafter to the indicated birth and death rates

PERIOD	PERCENTAGE BIRTH RATE IN PERIOD	BIRTHS IN PERIOD	PERCENTAGE DEATH RATE IN PERIOD	DEATHS IN PERIOD	POPULATION AT BEGINNING OF PERIOD
1	100	2.0	10	0.2	2.0
2	90	3.4	20	0 8	3.8
3	80	5.2	30	1.9	6.5
4	70	6.8	40	3.9	9.7
5	60	7.6	50	6 3	12 6
6	50	6.9	60	8 3	13.9
7	40	5.0	70	8.7	12.5
8	30	2.6	80	7 0	8.7
9	20	0.9	90	3.9	4.4
10	10	0.1	100	1.3	1.3

There are several ways in which an experiment on the growth of a *Drosophila* population can be carried out. Some of these ways differ in principle in a manner that is of importance in determining the kind of result obtained. The simplest case is to set up an experiment in the way described briefly above, and thereafter literally do nothing further except to let nature take its course and to count the flies at intervals. What then happens is that the population grows along a logistic curve for a little more than half of a complete cycle of such a curve. Then quite suddenly the population begins to decrease in numbers. This decrease goes on at an accelerating rate, until there are no survivors left.

The result is precisely that which is to be expected mathematically on the postulates that birth rates decrease and death rates increase uniformly at a constant linear rate. This is shown in table 2.

In the actual experiments the changes in the birth and death rates which lead to this type of curve, with first growth and then decline of population, are directly associated with the diminishing food supply under the conditions of a limited and closed universe.

The second type of experiment is one in which an attempt is made to add food as the supply is used up. The technical difficulties of doing this satisfactorily with a *Drosophila* population are considerable, but by sufficient care they can be overcome in large degree. The resulting growth of the population then follows a simple logistic curve, as I have described in detail elsewhere (8), and as is shown graphically in figure 9. There are two points in connection with experiments of this type which seem to need emphasis in the light of further work. The first is that, owing to the technical difficulties of adding new food to a bottle for reasons that are fully discussed in the reference cited, the food conditions are always suboptimal in experiments of this type. The second point is that the smoothness with which the populations follow the logistic curve in this type of experiment is probably a direct consequence of the fact just mentioned that the conditions as to food

are definitely sub-optimal. The nutritional level of the bottle is not high. It only a little more than barely permits *continued* growth of the population. Under these circumstances violent oscillations of either birth rates or death rates do not occur. The observations of population size lie smoothly on the logistic curve until the asymptote is nearly reached.

population. At the end of three days a census count is taken and the population is transferred to a new bottle, A_2, containing fresh new food to the same amount as was present initially in A_1. At the end of another three days a census count is again taken and the population again transferred to another bottle, A_3, which again contains new fresh food, and so on indefinitely. Meantime the lag bottles,

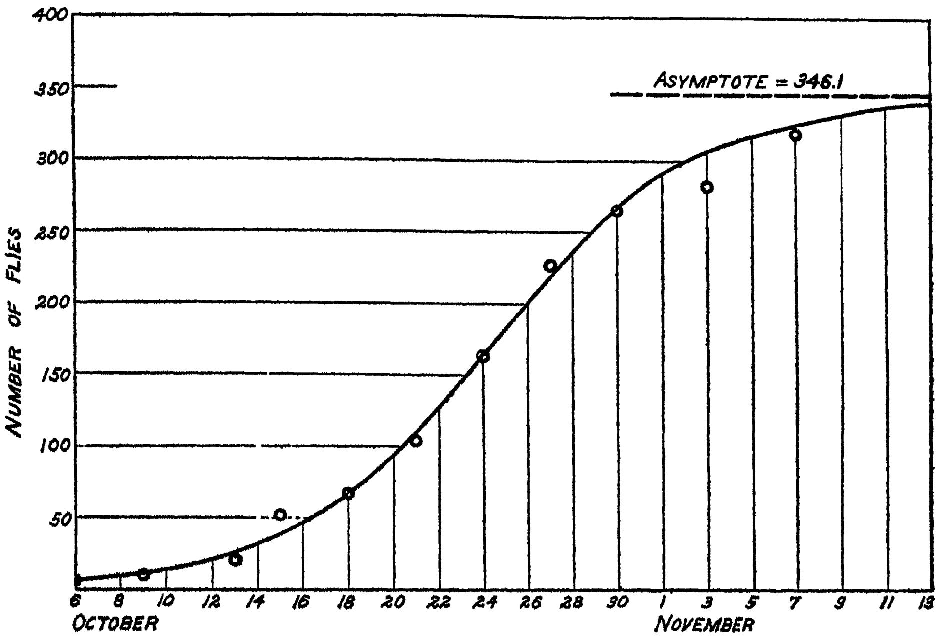

Fig. 9. Growth of an Experimental Population of Drosophila
The circles are observed census counts, and the smooth curve is the fitted logistic. (From Pearl (8))

The third type of experiment, which I here report on in a preliminary way for the first time, is so planned as to have the food conditions always optimal both as to quality and quantity. This is accomplished in the following way. Suppose a bottle A_1 to be prepared with our new synthetic food (9), which has been shown experimentally to lead to lower death rates and higher birth rates than any other natural or laboratory food tried, and to be seeded with an initial small

A_1, A_2, etc., which the adult population has left by transference, are examined daily. Whenever in any such bottle any flies hatch out from eggs which were laid by the females of the adult population while they were resident in that bottle, these newly hatched flies are counted (as births) and added to the adult population in whatever bottle it happens then to be. So then we get a record of the daily birth rate of the population. Also each day the bottle is examined in which

the adult population is actually then resident, and the deaths recorded. So then the situation in these experiments is that (*a*) there is a new and abundant crop of fresh food every three days, (*b*) all the young are born in a lying-in hospital and transferred to and counted into the general population only after they have been born and dried off there, and (*c*) there is complete registration of both births and deaths, as well as census counts of the population as a whole. The population is dependent upon any given single food supply only over a period of three days. During so short a period even the largest populations obtained do not begin to exhaust the food.

TABLE 3

Experimental data on the influence of density of population on rate of reproduction in Drosophila

PAIRS PER BOTTLE AT START	MEAN POPULATION 16 DAYS AVERAGE	IMAGOES PRODUCED PER FEMALE PER DAY. OBSERVED	CALCULATED NUMBER OF PROGENCY PER FEMALE PER DAY
1	2.00	21.4	21.1
2	3.40	12.6	14.5
3	5.50	10.8	10.2
4	7.32	9.1	8.1
5	9.29	5.9	6.7
6	10.29	6.8	6.2
7	11.51	5.2	5.6
8	14.48	4.6	4.6
9	16.62	4.1	4.0
10	18.74	3.1	3.6
12	21.70	3.5	3.1
15	26.02	2.3	2.5
20	34.02	2.2	1.8
25	47.75	1.0	1.1
30	47.73	1.2	1.1
50	90.66	0.33	0.34

Many experiments of this type have been performed. The general result is that the population first grows up to a maximum or asymptotic level, just as in the second type of experiment described above. But in this case the population can be kept at this asymptotic level as long as the experimenter desires. A striking result, however, is that both during the growth period and thereafter there are violent oscillations of the populations in size, about its mean position as given by the fitted curve. In fact these waves in the size of the population, produced by oscillations in the birth and death rates, are perhaps the most characteristic feature of population experiments of this particular type. It has not so far been possible to devise any method of holding these populations in a steady state at the level of the asymptote, when there is at all times an abundance of fresh food. The population simply waves up and down about an average size. I believe that this condition of unstable equilibrium is, in part at least, causally connected with the optimal food conditions. A detailed account of these experiments will be published, it is hoped, some time in the course of the next year.

THE EFFECTS OF DENSITY OF POPULATION

It has been stated above that the growth of a population along the logistic curve can be completely accounted for on theoretical mathematical grounds by making certain simple postulates regarding the relations between three variables, birth rate, death rate, and density of population. The basic postulate was that increasing density of population has associated with it adverse changes in birth rates and death rates. Is there experimental evidence in support of such a postulate?

For several years an intensive experimental investigation has been going on in my laboratory regarding the effect of density of population upon natality and mortality in *Drosophila*. The chief results of these studies may be briefly reviewed.

Some years ago Pearl and Parker (11) showed that if a count were made of the progeny (adult flies or imagoes) produced

in bottles of uniform size, uniform amount of food, and uniform air space, but with varying densities of population, the results were those shown in table 3.

These results are shown graphically in figure 10.

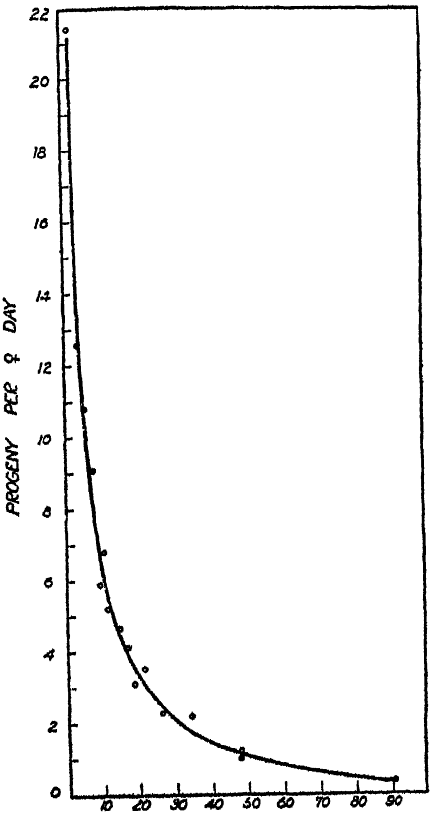

FIG. 10. SHOWING CHANGES IN RATE OF REPRODUCTION OF DROSOPHILA WITH INCREASING DENSITY OF THE MATED POPULATION

The circles give the observations and the smooth curve is the graph of the logarithmic equation discussed in the text.

There is evidently a profound and regular change in the rate of reproduction of *Drosophila*, under the conditions of these experiments, with increasing density of population. The number of progeny produced per female per day declines as density increases, at first extremely rapidly and then more and more slowly at higher densities. The total number of progeny flies (23,922) is large enough to give confidence in the results.

The last column of table 3 gives the calculated ordinates of the equation, fitted to the observations by the method of least squares,

$$\log y = 1.54 - 0.008\,x - 0.658 \log x$$

TABLE 4

Mean duration of life of Drosophila at different densities of population

INITIAL DENSITY	WEIGHTED AVERAGE MEAN DENSITY TO WHICH FLIES HAD BEEN SUBJECTED UP TO TIME OF DEATH	MEAN DURATION OF LIFE IN DAYS
2	1.77	27.31 ±0.58
4	3.30	29.32 ±0.60
6	5.00	34.45 ±0.65
8	6.68	34.20 ±0.61
10	8.15	36.22 ±0.72
12	9.72	34.31 ±0.61
15	12.42	37.92 ±0.66
20	16.69	37.07 ±0.55
25	20.68	37.47 ±0.49
35	28.85	39.43 ±0.67
45	37.23	37.46 ±0.51
55	44.65	40.04 ±0.53
65	53.16	35.25 ±0.45
75	59.66	32.34 ±0.46
85	66.95	30.10 ±0.36
95	74.50	27.17 ±0.36
105	80.36	24.20 ±0.32
125	94.38	19.60 ±0.28
150	111.88	16.17 ±0.24
200	144.47	11.93 ±0.20

where y denotes number of progeny flies produced per female per day over a sixteen-day period, and x denotes mean density of the mated population (measured as flies per bottle).

It is at once apparent that this equation describes the observed facts with extraordinary precision. Rarely, even in a physical or chemical experiment, does one get closer agreement between ob-

servation and theory than is here shown. Plainly the curve is the expression of the law relating these two variables, rate of reproduction and density. It is the inverse of Farr's law relating death rates and density in human populations (4, 1, 2).

These experimental results on the effect of density of population on the birth rate have been confirmed many times in my laboratory (*cf.* 10).

In all of these experiments so far mentioned the effect of density upon birth rates was measured by counts of adult progeny flies (imagoes) produced. This procedure left in doubt the point as to whether density produces its effect through an alteration of fecundity (egg production) or at some later stage in the process of reproduction. This doubt has now been cleared up by an elaborate series of experiments carried out in my laboratory during the past year by Dr. Arata Terao. In these experiments careful counts were made of the number of eggs produced under different densities of population. The results will shortly be published in detail. Here it is only necessary to say that they show conclusively that the primary effect of density, in populations of *Drosophila*, is upon fecundity (number of eggs laid). The number of eggs produced per female per day *decreases* with advancing density of population according to the same type of curve as that shown for progeny produced in the last column of table 3.

So then it may be concluded that increasing density of population does in fact have associated with it in experimental populations of *Drosophila* just the sort of adverse changes in the birth rate which were postulated in the theoretical discussion in the preceding section of this paper. Elsewhere (8) evidence has been presented showing that the same kind of effect of density is observable in populations of other organisms.

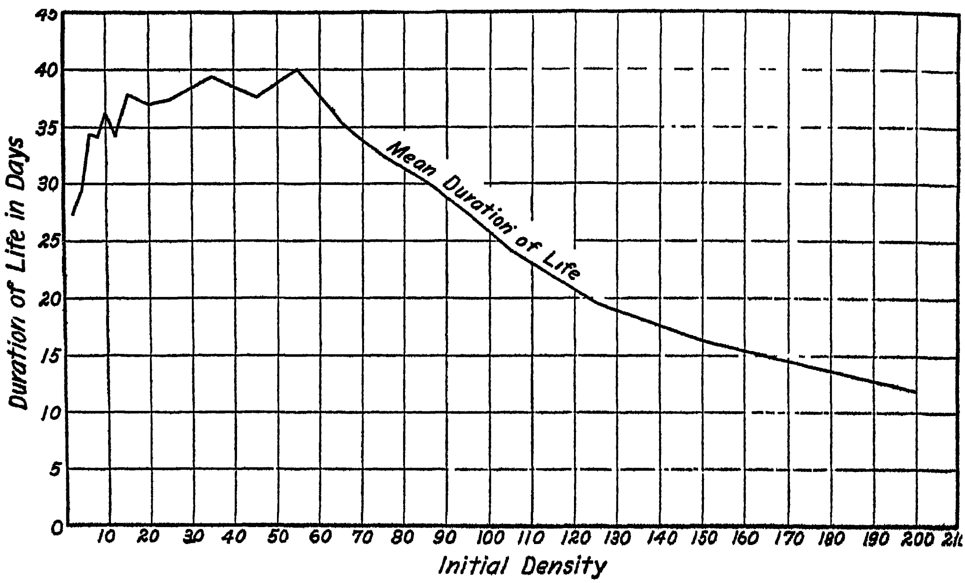

FIG. 11. MEAN DURATION OF LIFE OF WILD TYPE DROSOPHILA AT DIFFERENT DENSITIES OF POPULATION

The results of a large amount of experimental work regarding the effect of den-

sity of population upon *mortality* have recently been published in detail. Only the broad outcome can be presented here. This is done in table 4, which gives the mean duration of life in days of *Drosophila* subjected to the indicated densities of population. The experiments involved 13,000 flies. The results are shown graphically in figure 11.

What the figures in table 4 show is that after a density of 55 flies per one-ounce bottle is passed, the mean duration of life steadily decreases as density of population increases. Another way of putting the same thing is to say that the death rates in these experiments increased with increasing density of population after density 55 has been passed. The figures for mean duration of life are necessarily determined by the values of the death rates at ages. Other experiments have demonstrated that with extremely high densities of population the mean durations of life (or equally the death rates) approach an asymptote. In densities below 55, after a relatively small initial rise, there is little change in mean duration of life (or death rates) with small increases in density.

SUMMARY

To summarize: A large amount of mathematical, statistical, and experimental study has brought to light the following broad facts regarding the general biology of population growth:

1. Populations of organisms of the most diverse kinds, ranging from bacteria and yeast to man, are found statistically to follow in their growth a particular type of curve, the logistic.

2. Mathematical investigation shows that a curve of this type is necessarily generated under certain simple postulates as to the inter-relations between the two first-order variables, birth rates and death rates, and the second-order variable, density of population. One particular set of such postulates is that it shall be assumed, first, that birth rates are markedly affected adversely by small increases in density at relatively low densities, while after a certain density is passed further increases produce only slight decreases in birth rates down to an asymptotic limit; and, second, that death rates are insignificantly affected by increasing density at relatively low densities, while after a certain density is passed death rates markedly increase with increasing density up to an asymptotic limit.

3. Experimental investigation of populations of *Drosophila melanogaster* under controlled conditions shows that in fact the relations between density of population and birth rates, on the one hand, and density and death rates, on the other hand, which actually exist in such populations, are in accord with those theoretically assumed in the preceding paragraph. In short it is possible to account for all the main features of the growth of experimental populations of *Drosophila* by a simple hypothesis as to the correlated behavior of three variables.

A great deal more work needs to be done on the problem, and the investigations are being continued in my laboratory. The present paper is to be regarded only as a progress report. In condensed form it was read at the World Population Conference in Geneva, August 31, 1927, under the title "The Biology of Population Growth." It has been revised for publication in the QUARTERLY REVIEW OF BIOLOGY, and this publication is to be regarded as the definitive form of the paper.

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HOW NEAR IS THE RELATIONSHIP OF MAN TO THE CHIMPANZEE-GORILLA STOCK?

Address Delivered Before the Society of Mammalogists, April 29, 1927

By WILLIAM K. GREGORY

American Museum of Natural History

IT IS almost an axiom nowadays that to be orthodox in science one must make measurements and express his results in numbers. The old-fashioned sciences of comparative anatomy, classification and phylogenetics, partly because they did not make use of statistical methods of research, have been more or less despised and neglected by the younger generation and excluded from the elect company of the "exact sciences." But I would point out that arithmetic is not the sole branch of mathematics. Even historical sciences such as geology and palaeontology may claim an humble place in the mathematical hierarchy in so far as they succeed in discovering the sequence and relationships of events in time or space. When one determines that *a* is nearer to *b*, either in space, in time, or in a degree of similarity, than it is to *c*, and that *a*, *b*, *c*, are all nearer to each other than any of them is to *m*, *n*, *o*, then, provided always that his determinations are approximately correct, he has at least opened the way for a more precise evaluation of terms in the future.

The science of phylogenetics has sometimes been treated as an idle speculation, because it is supposed to be unable to test its hypotheses by direct experimentation. But a somewhat similar disadvantage lies upon the Egyptologist, who has nevertheless succeeded tolerably well in deciphering the documents available to him. An advantage of direct experimentation is that by means of the control experiments one can compare opposite conditions. But in historical sciences such as geology and phylogenetics the opposite to a given condition must be sought in nature. Nevertheless in many instances nature does provide the control experiment. In the study of mammalian evolution for example, we find that even today there are not a few animals in every large group that retain much of the primitive pattern that is known in their remote fossil relatives. These "living fossils," such as the existing opossum, correspond at least in part to the unmodified "control experiments" of the laboratory, while their highly specialized relatives, such as the kangaroos and the wombats, are nature's successful experiments in adapting an originally arboreal type to widely different methods of locomotion. Among the order of Primates, including all the known fossil and living types, there is an imperfect but still decipherable record of the branching out of a very remote stock of Upper Cretaceous and Paleocene age, from forms in general like the modern tree-shrews, into the various divisions of lemurs, cheiromyoids, lorisoids, tarsioids, platyrrhine monkeys, Old World monkeys, anthropoids and man.

At the present time the chimpanzee and

the gorilla differ from man in so many striking characters that Professor Osborn has recently written that the human family has been totally disconnected from the Simiidae since its earliest infancy. Denying the "myth" of man's descent from apes as due to our ignorance of the real course of human evolution, Professor Osborn holds that the existing apes have ape brains and ape minds, adapted for life in the forest, that they walk on all fours, that the human foot shows no evidence of derivation from an arboreal type, that when men climb they do so in an awkward un-ape-like fashion, that the Neanderthal race had descended from thousands of generations of upright-walking men, and finally, that man was already a tool-making, intelligent being in the Pliocene epoch, certainly more than one million years ago.

Fig. 1. Gorilla Foetus (After Deniker)

LIKENESSES OF MAN AND ANTHROPOIDS

In the face of this crushing indictment can anyone continue to defend the claim of the gorilla and the chimpanzee to be man's next of kin? Profoundly as I regret to differ from Professor Osborn, I must testify that my own studies of recent and fossil vertebrates have led me to somewhat different conclusions regarding the origin of man. In brief, as it appears to me, there is cumulative evidence for Darwin's view that man represents an early offshoot from the anthropoid stock, that he is descended from a thoroughly arboreal, tailless, upright-moving, brachiating pro-anthropoid and that the probable time of his first separation from the ancestors of the chimpanzee and the gorilla was hardly earlier than the middle of the Tertiary period.

Even an obstetrician might well be excused if he should mistake this (fig. 1) for a strange sort of human baby. It is Deniker's famous gorilla foetus. The adult gorilla runs on all fours, using its knuckles for supports, but this foetal gorilla is anything but a quadruped. We see at once that the gorilla agrees with man in having the anterior extremity modified into a true hand. Notice also the way the forearm is connected with the body across the broad chest, quite unlike the narrow deep chest of quadrupeds. Its whole general appearance is almost human. A careful comparison of the foetal gorilla with that of man (such as that by Deniker) affords the most cogent evidence that these two forms are relatively closely related in spite of the conspicuous differences in the adults.

Let us turn first to the locomotor apparatus. Here (fig. 2) we see a type of primate that was characteristic of the first half of the Tertiary epoch, one that has

persisted with little modification of the skeleton in certain of the existing lemurs of Madagascar. It was a long-tailed arboreal quadruped with grasping hands and feet, a relatively small brain and eyes that look outward as much as forward. From the construction of its backbone, pelvis and limbs I infer that when this animal leaped or ran it did so after the manner of quadrupeds, with its vertebral

FIG. 2. SKELETON OF *Notharctus osborni*, REPRESENTING A PRIMITIVE STAGE IN THE EVOLUTION OF THE PRIMATES. EOCENE, WYOMING

column nearly horizontal, and from the evident lack of ischial callosities I infer that it did not customarily sit upright as do the monkeys and apes of the Old World.

This animal (fig.3), on the contrary, represents a type of primate that was characteristic of the second half of the Tertiary period, and which from much anatomical and physiological evidence is known to be closely related to the human stem. It no longer holds its body in a horizontal position but at least in sitting and squatting the backbone is rotated upward at 90° to the primitive horizontal

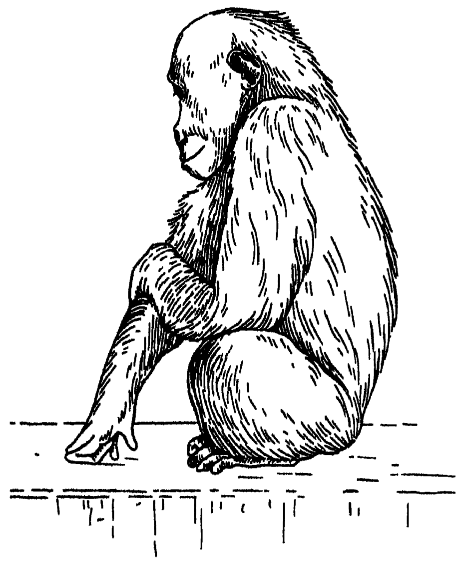


FIG. 3. YOUNG GORILLA IN SQUATTING POSITION (After Hagenbeck)

position and the head is balanced in this at first difficult position. It is quite tail-less, the vestigial caudal vertebrae forming a true coccyx, and some of the former tail muscles have now become enlarged to form a muscular floor of the pelvis. There is even an incipient lumbar curve in the back-bone. The eyes are now directed forward and the mouth is below the eyes rather than wholly in front of them. In these and a hundred other significant features this modified survivor of the Mid-Tertiary

anthropoid stock reveals its structural kinship to man. Even the external ear is thoroughly human except in quite minor details.

The adoption of the upright sitting posture and the suspension grasp of a tree-climbing life changed a forefoot into a true hand. Too long continued specialization in this line has changed the orang's hand into a hook, but our own ancestors were driven out of their arboreal paradise before they yielded too far to its transforming spells.

The chimpanzee, it is true, has a hand with a reduced thumb, or rather with unduly elongate fingers, but in view of this figure (fig. 4) by the eminent zoologist J. E. von Boas, can any one doubt that the chimpanzee has a true hand and that it belongs to a division of the higher primates characterized by having the anterior extremities modified as hands rather than as forefeet?

And while the chimpanzee thumb may be reduced, all the available evidence forbids us to look for a thumb as

FIG. 4. HAND OF CHIMPANZEE AND OF MAN
(After J. E. von Boas)

large as this in the remote ancestors of man.

Professor von Boas has also shown that the arrangement of the extensor and flexor tendons in the hand of the chimpanzee is peculiarly human in appearance.

FEET OF APES AND MAN

Turning again to Deniker's gorilla foetus (fig. 5), we see that not only does the gorilla agree with man in having the anterior extremities modified as hands but the hind feet are fundamentally human in structure, differing chiefly in the lesser reduction of the second to the fifth toes and in the divergence of the great toe.

The divergent great toe of the chimpanzee and gorilla has been an occasion of stumbling for the numerous authors that have been unable to see that the human foot is essentially an anthropoid foot with the great toe brought parallel with the others.

This record (fig. 6) of the Mountain Gorilla foot by Akeley has been impugned by Sir Ray Lankester precisely because this foot appeared too human and because he (Lankester) had never seen its like before. But there it stands, and there (fig. 6) is the opposite foot of the same species. In this instance Nature has supplied us with an experimental demonstration of the initial changes necessary to adapt a gorilloid foot in the human direction.

But if the foot of the Mountain Gorilla approaches that of man, the foot of a human foetus of the ninth week, figured by Professor Schultz, assuredly recalls the anthropoid type in so far as its great toe is widely divergent from the others. In the large size of the great toe this foot differs widely in appearance from the foot of primitive Eocene placental mammals other than primates.

An excellent reason for the dominance of the great toe in man, is that in all known primates from the lower Eocene onward the great toe is the anchor or pivot for very strong muscles and tendons of locomotion. The powerful flexors of the great toe aid, even in the oldest primates, in raising the weight of the body, while the great tendon of the peroneus longus muscle was inserted into the strong process on the proximal end of the first

FIG. 5. GORILLA FOETUS. SIDE VIEW
(After Deniker)

metatarsal in all known primates from Eocene lemuroids to man.

Hence it seems quite legitimate to infer that when the human foot was made over for use on the ground the same powerful flexor and peroneus muscles of the great toe still served to raise the weight of the body. Moreover, the transverse muscles of the anthropoid foot were used on the ground in preventing collapse of the trans-

FIG. 6. FOOT OF THE MOUNTAIN GORILLA (GORILLA BERINGEI)

A, skeleton of foot. *B*, right foot after removal of skin. *C*, cast of foot from freshly killed animal, made by the late Carl E. Akeley

verse arch, while the powerful adductor of the hallux assisted in drawing the hallux toward the other digits.

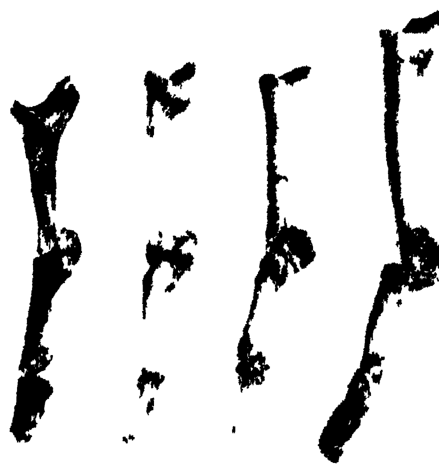
Professor Schultz's researches (1926) on the growth stages of primates have brought strong support to Darwin's view of the close relationship of man to the anthropoid stem. His figure brings out the extraordinary resemblance of the late human foetus to the gorilla. These figures even suggest that man diverged from the gorilla branch after the separation of the chimpanzee and that thereafter the gorilla and man rapidly became extremely different, the former becoming quite secondarily a great-jawed, gigantic quadruped, the latter, a weak-jawed biped. The characters of the brain, ear, etc., are in harmony with this view.

It has been suggested, by myself and others, that some of the characters common to man and one or more of the anthropoids may well be due to "parallelism," that is, to the independent acquisition of similar characters after the divergence from a common stock; but in view of the many positive agreements the burden of proof must rest upon those who would class all of the resemblances as "parallels." In fact, the special resemblances between man and ape, outside of those common to typical mammals, are found in so many different parts of the organism, that the assumption of such extensive parallelism is a mere begging of the question.

STRUCTURAL AND CHRONOLOGICAL KINSHIP

The question, how near is the relationship of man to the chimpanzee-gorilla stock, may be intended in two different senses. We may be thinking either of man's structural kinship, in which case the question may be answered by recounting the degree of resemblance in respect to the different morphological or physiological characters under consideration, or we may be thinking of the degree of kinship in respect to the distance in time back to a common stock and the number of generations since the divergence, along each of the branches. This brings us to the subject of the antiquity of the human family.

Professor Osborn has very forcefully presented the evidence for the existence of



A *B* *C* *D*

FIG. 7. HALLUX OF FOSSIL AND RECENT PRIMATES, SHOWING PROCESS FOR INSERTION OF TENDON OF PERONEUS LONGUS MUSCLE

A, *Notharctus tyrannus*, Eocene *B*, *Lemur mongoz*, Recent. *C*, *Cebus capucinus*, Recent. *D*, *Macacus sp.*, Recent

man, as such, in the Pliocene epoch, and he points out that under the newer currently accepted estimates of geologic time man's proved antiquity is at least twenty times greater than it was formerly thought to be.

But in the first place, a good part of this apparent increase is due to the fact that the newer estimates of the length in years of the geologic time epochs are from ten to twenty times longer than the old estimates. Thus the beginning of the Eocene

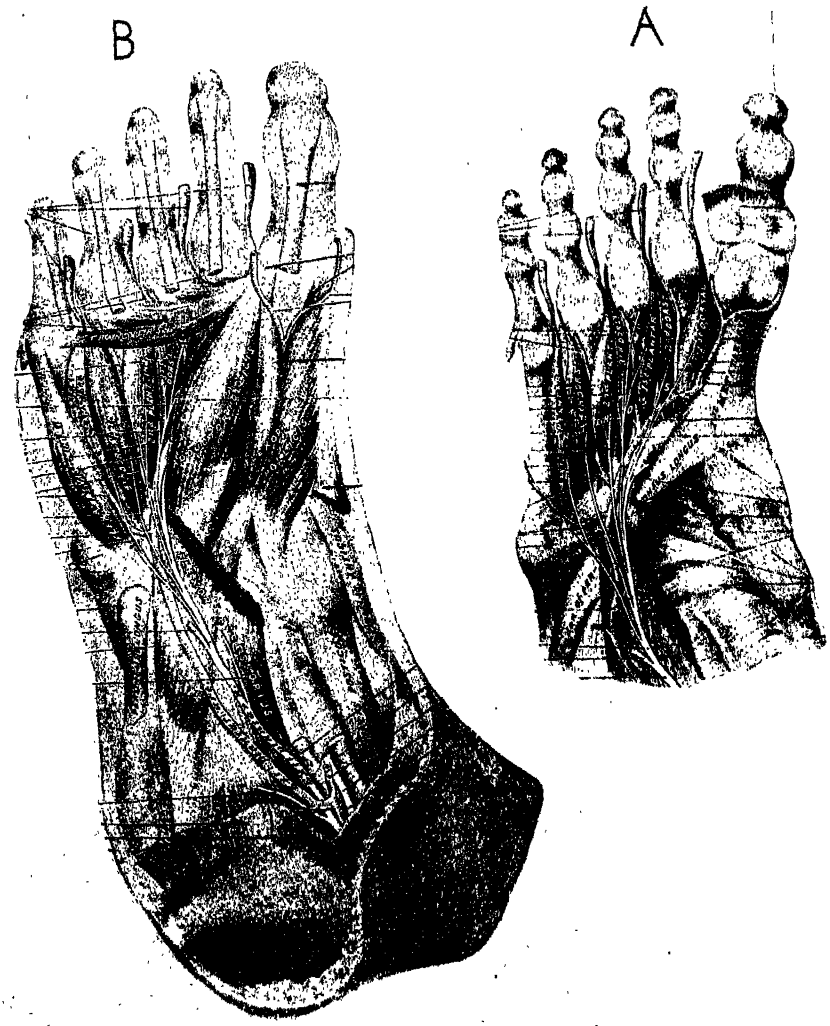


FIG. 8. ANTHROPOID HERITAGE IN THE HUMAN FOOT

A shows insertion of tendon of peroneus longus on proximal end of metatarsal of great toe. *B* shows transversus and flexor hallucis muscles. (After Weisse)

epoch, formerly reckoned as 3,000,000 years ago, is now set back to 60,000,000 years.

Secondly, figure 9 shows that if we accept Barrell's estimates of the length in years of the successive epochs of the Tertiary period, the relative antiquity of the oldest known human fossils as compared with that of various other known fossil primates is as follows:

Man	1 to 3 million years
Dryopithecus	5 to 7 million years
Propliopithecus	33 million years
Eocene Primates	38 to 60 million years

Thus, while the antiquity of man may be twenty times longer than it was formerly

thought to be, yet it is at most only one-twentieth the antiquity of the earliest known fossil primates.

Professor Osborn infers that because some Pliocene horses were almost like modern horses, all Pliocene men were essentially human. Because *Eohippus* had already started on the long road toward *Equus* in the Lower Eocene, the ancestral pro-man already existed in the Oligocene. These deductions, Professor Osborn fervently believes, will be vindicated by future discoveries in Central Asia.

Professor Osborn also believes that because evolution is irreversible no line of apes could ever change into men, since their entire psychology and functions would predestine them to become "super-apes." According to his view, the habit of brachiation which is regarded by Keith and by Gregory as one of the chief prerequisites for both anthropoid and human origin, must lead only to the reduction of the thumb and the transformation of the hands into hooks. But taking a broad view of the animal kingdom, we find not a few instances in which living organisms have broken away from the straight and narrow path of orthogenetic specialization; in new environments they have changed the trend of their evolution and escaped into new evolutionary possibilities. Such radical changes of habitat, as when various lines of marine reptiles and marine mammals were derived from originally terrestrial stocks, always involve profound changes of function. And it is obviously the principle of the change of function which must have been exemplified, no matter from what infra-human source man has been derived.

The myology and osteology of the whole pectoral limb of man constitute a veritable palimpsest, bearing a clearly decipherable record, first, of an earlier period when every bone and muscle was adapted for the habit of supporting the body weight by the uplifted arms, and secondly, of a later stage when the arms were no longer used for locomotion but for the support and manipulation of ob-

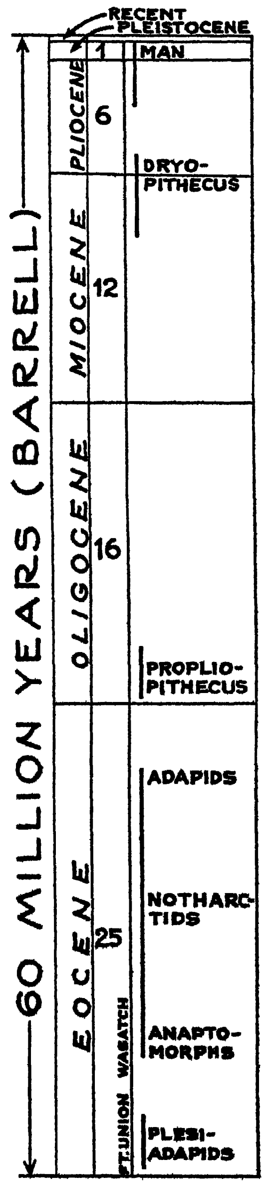


FIG. 9. THE ANTIQUITY OF MAN COMPARED WITH THAT OF OTHER PRIMATES; TIME ESTIMATES (AFTER BARRELL) IN MILLIONS OF YEARS

jects held in the hands. Obviously it is not necessary to infer that in the ancestral anthropoid the extreme specializations for brachiation had already taken place. Great difficulty has been experienced from the fact that in modern man the arms and hands are relatively shorter and the legs relatively longer than in modern apes. This failure to realize that readjustments of proportions have constantly been taking place, especially when profound changes of function were involved, thus leads to the error of expecting a generalized ancestral stock to exhibit the specialized proportions of some one of its remote descendants. Also, Schultz has cited embryological evidence tending to show that the lengthening of the legs in man is a relatively recent acquirement, perhaps correlated with the ground-living cursorial habit.

From the study of all the still surviving families of primates it has been inferred (Gregory, 1920) that, starting from arboreal tree-shrew-like forms, the primates passed through a stage not unlike the lemurs in many general characters, particularly of the brain and skeleton, that they then went on to the primitive monkey stage and then, progressing through an upright sitting stage, gave rise to the pro-anthropoids, which in turn gave rise to the diversely specialized recent anthropoids, and to man. The direct palaeontological evidence, so far as it goes, appears to be in complete harmony with this view and with no other known to me.

The cumulative evidence from many independent sources establishes the high probability that the anthropoid apes are man's next of kin, not only in embryonic development, adult organization and physiology, but also in the sense that the separation of the human and great ape stocks was a far later event in geologic time than the separation of the horse family from the tapir family in the Lower Eocene.

CONCLUSIONS

In brief, I submit the evidence recorded in my previous papers together with the considerations advanced in the present paper, in support of the following conclusions:

I. Considering the evidence afforded by comparative studies on the brains of primates, the anthropoid apes as a whole are undoubtedly man's nearest known relatives, the order of structural relationship being: (1) modernized man; (2) primitive man; (3) gorilla; (4) chimpanzee; (5) orang; (6) gibbon; (7) Old World monkey; (8) New World monkey; (9) *Tarsius;* (10) lemur; (11) pentailed tree-shrew (Elliot Smith, Tilney, Le Gros Clark). Modern students are also convinced that the general order of evolution was the reverse of this, namely, from primitive tree-shrew to lemuroid, to stem tarsioid, to pro-anthropoid, to man.

II. Considering the evidence afforded by the comparative study of the teeth of all known recent and fossil primates, the order of structural evolution is as follows: (1) Generalized tree-shrew (*cf.* Paleocene, *Indrodon*); (2) primitive lemuroid (*cf. Pelycodus ralstoni*, Lower Eocene); (3) primitive tarsioid (*Parapithecus*, Lower Oligocene); (4) proto-anthropoid (*Propliopithecus*, Lower Oligocene); (5) primitive anthropoid (*e.g. Dryopithecus rhenanus*); (6) primitive man (*e.g. Eoanthropus*); (7) modernized man (*Homo sapiens europaeus*).

Among existing primates the general order of resemblance to man in the dentition is: (1) chimpanzee; (2) orang; (3) gorilla; (4) gibbon; (5) *Tarsius*.

III. Dr. Gerrit S. Miller and Professor Wood Jones seem to have over-emphasized the fact that the known remains of fossil

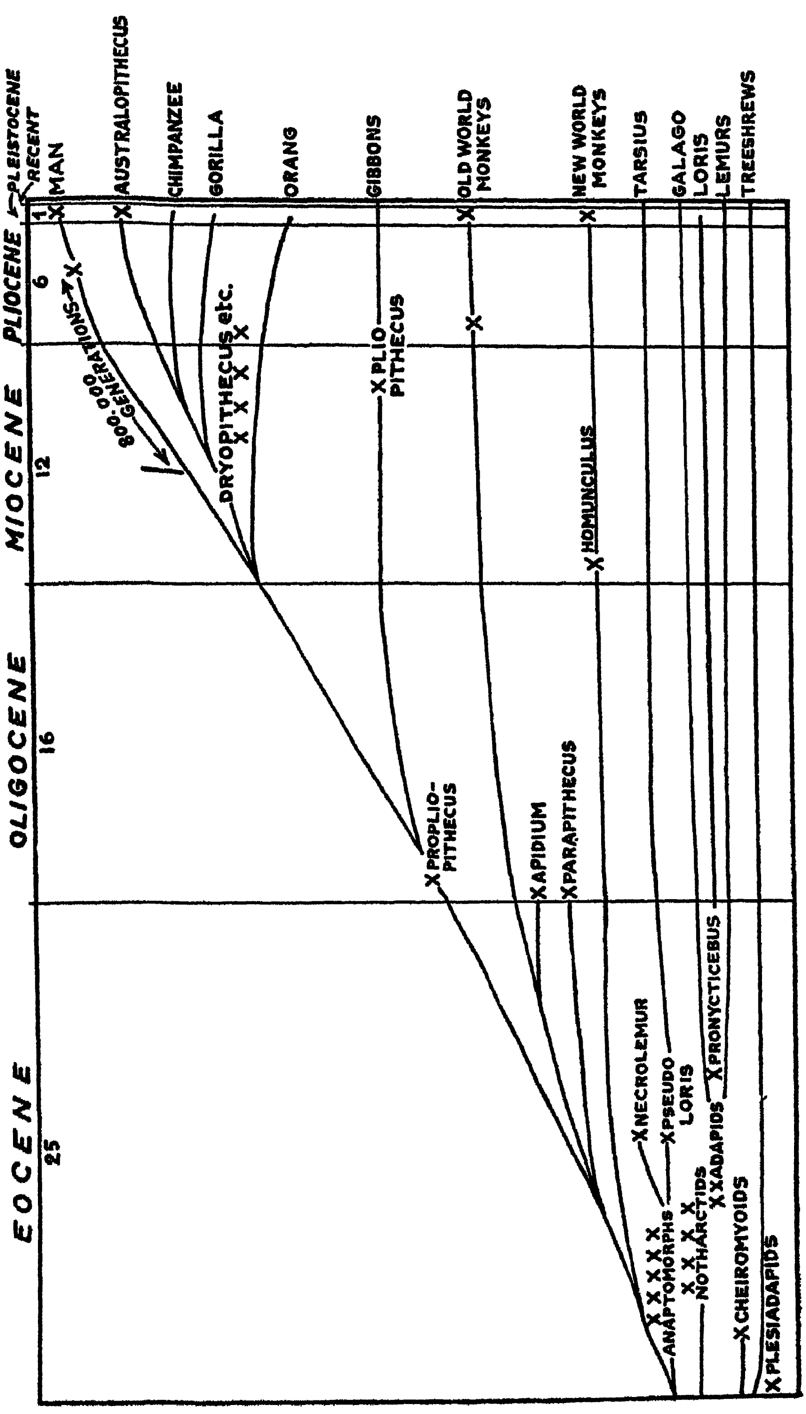


Fig. 10. Tentative Phylogeny of the Primates

anthropoids consist mostly of broken jaws and teeth. Apparently they think that because the specimens are broken and imperfect, any conclusions based on them must be equally defective. But these specimens, imperfect as they are, supply highly important and significant landmarks in the evolution of the primates and when considered in the light of the great body of evidence from anatomy, embryology, physiology, they are sufficient to establish a high degree of probability that the separation of man from the anthropoid stock did not occur before the middle of the Tertiary period.

IV. Turning to another aspect of the question, how near is the relationship of man to the chimpanzee-gorilla stock, we have to ask: About how many generations may have existed since the final separation of man from the anthropoid stock, that is, since interbreeding between the two ceased. Assuming that this occurred in the Middle Miocene, that would give a period of about ten million years to the Upper Pliocene *Eoanthropus*. The anthropoids approach sexual maturity at ten years of age, while certain races of men can breed at twelve years. Assuming twelve years, or about eight generations to a century as the average rate, that would give 800,000 generations as the transitional period between *Dryopithecus* and the Piltdown man.

Dr. Gerrit S. Miller once said that if the divergent great toe of a chimpanzee were to be pressed around so as to be parallel with the other toes, it would cause the animal intense pain and that he would therefore not walk in such a way as to produce such pressure. Hence a chimpanzee-like foot could never be changed into a human foot. But even an acute pain, divided among 800,000 generations, might be supportable. In other words, much might be done toward bridging the remaining gap between some member of the *Dryopithecus* group and man during 800,000 generations, especially in view of the relatively high structural variability of all the known races of man and of anthropoid apes.

In conclusion figure 10 is submitted as a tentative answer to the question: How near is the relationship of man to the chimpanzee-gorilla stock?

POSTSCRIPT

Since this paper was written Professor Osborn has definitely accepted the remote arboreal ancestry of man and ascribes the common characters of man and anthropoids mostly to inheritance from a "neutral" stock, the "Anthropoidea" of the Oligocene and Eocene. He again protests against the use of the word ape in connection with any human ancestor, insisting that the word be limited to the modern specialized forms.

NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of biology. In addition there will usually appear in each number one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to Dr. Raymond Pearl, Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *1901 East Madison Street, Baltimore, Maryland, U. S. A.*

BRIEF NOTICES

EVOLUTION

THE DISTRIBUTION OF BIRD-LIFE IN ECUADOR. *A Contribution to a Study of the Origin of Andean Bird-Life. Bulletin of The American Museum of Natural History, Vol. LV, 1926.*
By Frank M. Chapman.
The American Museum of Natural History
$6.00 *New York*
6¼ x 9¼; xiii + 784 (paper)

This report embodies the results of ten years work of Dr. Chapman and his assistants on the birds of Ecuador. Like his earlier volume on the bird life of Colombia, it is a monumental contribution to systematic ornithology, geographical distribution, and evolution. The conclusions regarding evolution are of great interest. Dr. Chapman says:

> So I might continue to present evidence illustrating the dependency of evolution on change of environment, but I may sum up my case by offering the entire avifauna of Ecuador as an exhibit. What more adequate tribute to the power of environment can one ask than to discover within this comparatively small but marvelously diversified country one-fourth the birds of all South America and one-twelfth those of the entire world?
>
> In the face of these facts, of the significance of which prolonged field experience has convinced me, I am asked to believe "that chance mutation is quite sufficient to account for all organic evolution," that "environment permits and directs evolution but does not cause it."
>
> Environment, we are told, cannot affect the germ plasm; that its influence therefore is not hereditary; and that only those mutational variations arising within the chromosome can be transmitted.
>
> It is when environment acts through climate or through food, for example, that it apparently produces a change on the organism in which selection has no part, though it must later determine whether such change is desirable.
>
> Whether environment originates or whether, in the language of the day, it merely "starts something" by arousing latent potencies within the germ, I do not pretend to say. But the fact remains that organisms do respond to change and, furthermore, that certain conditions, for example, humidity and aridity, almost invariably provoke the same type of response. Whether the changes are favorable or unfavorable, it remains for environment to decide.
>
> I believe, therefore, that first, as well as last, evolution is largely the product of environment, particularly of change of environment, with its more or less direct action on the organism and its rejection or retention of the resulting characters.

ENVIRONMENT OF THE TETRAPOD LIFE IN THE LATE PALEOZOIC OF REGIONS OTHER THAN NORTH AMERICA. *Carnegie Institution of Washington, Publication No. 375.*
By E. C. Case.
Carnegie Institution of Washington
$2.50 *Washington, D. C.*
9 x 12; iii + 211 (paper)

The final conclusion of this thorough piece of paleontological research is of much interest and significance to biologists in general and geneticists in particular:

While the author has no suggestion as to the method of evolution, and has no concrete instances to offer in evidence, he is impelled to record here his conviction that the environment is in some way a fundamental factor in the progress. In common with every paleobiologist who has considered evolution in the perspective of time and environment, this conviction is forced upon him. That there are fundamental progressive changes developing independent of the environment through long time, there can be no doubt. That there are series of changes very similar in character, often and consistently repeated, and closely related to synchronously repeated environmental changes, seems equally beyond question. Until the results of the experiments of the neobiologists have stood the test of time, a test which they neglect or sadly undervalue, the author is content to say that, in his opinion, for all adaptive evolutionary changes, the environment either induces the result or acts as the selective screen which determines what forms shall survive and what perish; the environment determines what path life shall take. Whether this statement applies to the major and fundamental changes which have separated the higher groups, even the paleontologist has not as yet the grasp of the effect of time and cosmic environmental changes to venture an opinion.

MIND IN EVOLUTION.
By L. T. Hobhouse. *The Macmillan Co.*
$4.25 *New York*
$5\frac{1}{2}$ x $8\frac{3}{4}$; xix + 483

A reprint, without textual alteration, of the second edition of this standard work. There are added two brief new appendices. The first defends the author's use of the term "correlation" as "at once more general, more plastic, and more significant of mental activity," than the now popular *Gestalt* of the German psychologists. The second new appendix deals with "Instinct in Man," and expands the discussion in the text.

ADAPTIOGENESE UND PHYLOGENESE. *Zur Analyse der Anpassungserscheinungen und Ihrer Entstehung.*
By Albert Eide Parr. *Julius Springer*
Rm. 4.20 $6\frac{1}{2}$ x $9\frac{1}{2}$; 60 (paper) *Berlin*

This is the first number of a new series of *Abhandlungen zur Theorie der organischen Entwicklung*, which has been established as a continuation of Roux's *Vorträge und Aufsätze über Entwicklungsmechanik.* The author is of opinion that the genesis of adaptions is a wholly separate phenomenon from phylogenesis, and that there is no need to postulate any adaptive tendency in phylogenesis. The relation of the selection principle to the origination of adaptations is critically discussed. There is no index.

DER ARTENWANDEL AUF INSELN *und Seine Ursachen ermittelt durch Vergleich und Versuch an den Eidechsen der Dalmatinischen Eilande, by Paul Kammerer. Nebst einem Anhang: Zur Systematik der Adriatischen Insel-Eidechsen, by Otto Wettstein.*
Franz Deuticke
30 marks *Leipzig*
$6\frac{3}{4}$ x $10\frac{1}{4}$; xiv + 324 + 8 plates (paper)

This was Kammerer's last book before his death. It deals exhaustively with variation in the lizards of the Dalmatian islands. Prof. MacBride says (Science Progress, 22: 307) that it "is one of the

finest contributions to the theory of evolution ever written, and deserves to rank with the *Island Life* of Wallace."

GENETICS

VARIABILITÄT UND VARIATION.
By Jur. Philiptschenko.
Gebrüder Borntraeger
5.70 G.M. *Berlin*
$6\frac{1}{2}$ x 10; 101 (paper)

The distinguished professor of genetics in the University of Leningrad reviews here the whole question of the different kinds of variation, and attempts to evaluate their significance in evolution. There is little that is novel in the book, but it is a timely, temperate, and well-balanced discussion of a problem of theoretical biology which, as Philiptschenko himself says, cannot possibly be really solved until we have at hand a vastly broader factual basis, especially experimental, than is now available. There is a bibliography of 6 pages, but no index.

GENERAL BIOLOGY

PRINCIPLES OF SOIL MICROBIOLOGY.
By Selman A. Waksman.
The Williams & Wilkins Co.
$10.00 6 x 9; xxviii + 897 *Baltimore*

A colossal piece of text book writing, which has not only technical interest and value for professional soil biologists, but also will be an extremely useful reference work for the general biologist, who has too long completely neglected the fauna and flora of the soil. If he will read this book he will find that a lot of things are going on there which have great theoretical interest. Dr. Waksman is to be congratulated on having produced so thorough and comprehensive a handbook of the field of biology.

THE MIGRATIONS OF BIRDS.
By Alexander Wetmore.
Harvard University Press
$2.50 5 x $7\frac{1}{2}$; viii + 217 *Cambridge*

The material included in this volume constituted a series of Lowell Lectures in Boston. It furnishes a most interesting and valuable review of the present state of knowledge regarding bird migration, one of the most fascinating problems of animal behavior, to the solution of which Dr. Wetmore by his own investigations has contributed much.

EXTRACTS FROM HOOKE'S MICROGRAPHIA. (*First Printed in London in 1665, Reissued by Permission of the Alembic Club of Edinburgh, with Additional Observations on the Cellular Structure of Plants as Revealed for the First Time by the Microscope Constructed by Robert Hooke of Christ Church in Oxford. Old Ashmolean Reprints VI.*)
Old Ashmolean
3 shillings $4\frac{3}{4}$ x $7\frac{1}{2}$; 60 *Oxford*

This entertaining little reprint of choice bits from the chief work of a versatile genius was prepared as a memento for members of the meeting of the British Association in Oxford in 1926.

DONNÉES NUMÉRIQUES DE BIOLOGIE ET DE PHYSIOLOGIE ET CHIMIE VÉGÉTALES. *Extrait du Volume V, Tables Annuelles de Constantes et Données Numériques.*
By E. F. Terroine and H. Colin (preface by

Léon Fredericq). *Gauthier-Villars et Cie.*
56 francs *Paris*
$8\frac{1}{2} \times 10\frac{1}{2}$; vii + 138 (paper)

Tables of constants, mainly chemical, over a wide and highly scattered series of biological phenomena. It will be found a useful reference work in every biological laboratory.

HUMAN BIOLOGY

TOWARDS THE OPEN. *A Preface to Scientific Humanism.*
By Henry Chester Tracy (with an Introduction by Julian Huxley.) *E. P. Dutton and Co.*
$3.50 $5\frac{3}{4} \times 8\frac{5}{8}$; xx + 257 *New York*

This is a contribution to the philosophy of human biology, by one who is not merely a biologist but has backgrounds—in philosophy, in art, and in humanism generally. While what is said is, by and large, not altogether new, it is extremely well said. Even Faguet never turned a neater one than: "Efficiency exhausts itself in the making of motions by which the illusion of accomplishment is maintained."

The central thesis of the book is that man, by his own stupidity, has taken most of the joy out of living, for all but a relatively few people, and even they have their difficulties in the face of the devastating social inheritance we have managed to load ourselves down with.

"'The open,' towards which we are moving, is a more natural and a freer life in which a man's responsibility is measured by his real relation to his social-natural environment (as shown by the allied sciences bearing on that relation), and his value is measured by his real capacity, discovered under treatment to which he is entitled as a man."

We hope that Mr. Tracy will write some more.

TYPES OF MIND AND BODY.
By E. Miller. *W. W. Norton and Co., Inc.*
$1.00 $4\frac{1}{4} \times 6\frac{1}{2}$; 95 *New York*

An entertaining brief review of the modern "constitution" theory, so much to the fore just now in medicine. Don Quixote and Sancho Panza serve once more as the paradigmatic asthenic and pyknic respectively; indeed the author dedicates his book to Cervantes with the statement that it is "merely a footnote" to that great man's portraits of these two worthies. Dr. Miller's general position is that: "in order to envisage the whole character of man we must view him, not as body nor as mind, but as an integrated dynamic system of forces which in its inheritance and its own history weaves the fabric of Personality."

This seems sounder doctrine than some we have heard from the constitutionalists.

LA FORCE MOTRICE ANIMALE *à travers les âges.*
By Lefebvre des Noëttes. *Berger-Levrault*
20 francs *Paris*
$5\frac{1}{2} \times 9$; viii + 138 + 80 plates (paper)

An interesting piece of archeological and historical research on the evolution of the use of living organisms to furnish motive power to aid man in his enterprises. It is beautifully illustrated with 217 figures on 80 plates. The author distinguishes two periods in the evolution of transportation by animal motive power. In the first man himself was the only efficient motor. In the second period the more effective utilization of animals as sources of motive power freed man from such toil, and paved the way for the

development of mechanical motors. The book is an entertaining contribution to human biology.

A STUDY OF BRITISH GENIUS

By Havelock Ellis. *Houghton Mifflin Co.*
$3.50 $5\frac{1}{2} \times 8\frac{3}{4}$; xvi + 396 *Boston*

A new edition of a book originally published over twenty years ago. There is no important change from the original form, the author having concluded after deliberation that he cared to make none. There are, however, four new chapters, which follow the "General Conclusions" of the original study. They deal respectively with "The Celtic Spirit in Literature," "The Evolution of Painting in England," "Genius and Stature," and "The Comparative Abilities of the Fair and the Dark." The book is fully documented and indexed. Its reissue in enlarged form is a real service to students of human biology.

OUR EARLY ANCESTORS. *An Introductory Study of Mesolithic, Neolithic, and Copper Age Cultures in Europe and Adjacent Regions.*

By M. C. Burkitt. *The Macmillan Co.*
$2.50 $5\frac{1}{4} \times 7\frac{1}{2}$; xii + 243 *New York*

A welcome addition to the literature of prehistory, by a master in the field. The overwhelming interest in recent years in paleolithic man and his works has diverted attention from our nearer ancestors of neolithic times. The topical divisions of the subject matter are as follows: mesolithic times; neolithic civilization; typology (of artefacts); neolithic cultures of the eastern area and late neolithic times in central Europe; neolithic cultures of the northern and western areas; England in mesolithic, neolithic, and earliest metal age times; the Mediterranean area and the copper age; bronze age cultures. The book is well illustrated and indexed.

HAIR. *With Special Reference to Hypertrichosis.*

By C. H. Danforth.
American Medical Association
$6\frac{3}{4} \times 10$; 152 *Chicago*

This book is a review of the literature, and of the researches of the author and his colleagues regarding human hair. The topics treated are: The phylogeny of hair; The hair of mammals; General characteristics of human hair; Regional characteristics of human hair; Factors affecting the growth of hair; Aberrant forms of hair growth; Hypertrichosis; General aspects of the hair problem. There is a bibliography covering 7 pages. The work is a valuable contribution to anthropology.

THE RACIAL BASIS OF CIVILIZATION. *A Critique of the Nordic Doctrine.*

By Frank H. Hankins.
Alfred A. Knopf, Inc.
Trade edition $3.75 *New York*
Text edition $2.75
$5\frac{1}{4} \times 8$; xi + 384

The professional Nordics have been encountering very heavy weather of late in their noble voyage to get us safely *into* the trenches of embattled race prejudice by Christmas. Now, in Professor Hankins' book, their ship meets a veritable typhoon. Unless help is rushed to the scene promptly we judge that all of the crew except those who are so oily that surface tension saves them will be *spurlos versenkt.* For Hankins is a rough fellow, and does not spare even Important Persons. We only wish that he had been a little

bit more critically discriminatory in respect of the character of some of the evidence which he accepts as furthering his argument.

GRUNDRISS DER KRIMINAL-BIOLOGIE.

By Adolf Lenz *Julius Springer*
Reichsmark 15 *Wien*
6 x 9¼; vii + 252 (paper)

A study of the personality of criminals by the technique of modern "constitution" theory. It is a careful piece of work, well illustrated and documented. Many case histories are presented in considerable detail. The author's position is that a criminal act is to be regarded as the kinetic expression in actuality of a corporeal-spiritual potentiality, which is the total "personality" of the individual, under the influence of the environment. This seems to differ from the average police sergeant's estimate of the nature of criminality only in the nobility of the language in which it is expressed.

BIRTH INJURIES OF THE CENTRAL NERVOUS SYSTEM. *Part I—Cerebral Birth Injuries*, by *Frank R. Ford*. *Part II—Cord Birth Injuries*, by *Bronson Crothers and Marian C. Putnam.*

The Williams & Wilkins Co.
$4.00 6 x 9; xiii + 164 *Baltimore*

Aside from its considerable obstetrical and psychiatric interest, this volume has a good deal of significance for the thoughtful eugenist. It demonstrates that not a few of the nervous and mental disturbances of later life, which in the normal course of a eugenic investigation get a black mark in the pedigree and are used to elucidate the location of a gene, have nothing whatever to do with genes but are simply expressions of unfortunate obstetric accidents.

RUSSEN UND CHINESEN IN OSTSIBIRIEN.

By Wladimir K. Arsenjew.

August Scherl G. m.b.H.
9.50 gold marks 6 x 9; 228 *Berlin*

The Ussur region of Eastern Siberia, bordering the Japanese Sea, has an interesting mixed population of Chinese, Russians, Koreans, and "natives." This interesting volume discusses in considerable detail the economic and social life of this population, with especial reference to their industries. The book is quite extensively illustrated with photographs. Perhaps its greatest interest is for the geographer.

AMERICAN AGRICULTURAL VILLAGES.

By Edmund deS. Brunner, Gwendolyn S. Hughes, and Marjorie Patten (Institute of Social and Religious Research).

George H. Doran Co.
$3.50 5½ x 8½; 326 *New York*

A statistical and sociological study of 140 agricultural villages, ranging in population from 250 to 2500, and scattered over the whole United States, with heaviest incidence of the selection in the eastern part of the country. It continues the two earlier village studies made by the Institute of Social and Religious Research. It is a useful social document, well indexed.

L'HÉRÉDITÉ MUSICALE.

By Louis Vezoux. *E. le François*
25 francs 6½ x 10; 279 (paper) *Paris*

The conclusion of this thesis for the doctorate is that it is heredity alone which makes the musician. Education and the environment merely perfect his talents. There are no new observations, the basis for the conclusions being found chiefly in the writings of American investigators in this field.

CHINA. *A Commercial and Industrial Handbook. Department of Commerce, Bureau of Foreign and Domestic Commerce. Trade Promotion Series No. 38.*
By Julean Arnold, American Consular Officers, and Other Contributors.
Government Printing Office
$1.75 *Washington, D. C.*
$5\frac{3}{4}$ x 9; xvi + 818

No student of the population problem ever gets far in the exhortatory moiety of his lucubrations without dragging in China. While prepared for quite another group of earnest workers this extremely detailed picture of the environmental elements, physical and biological (including social and economic), which operate upon the Chinaman will be found a useful reference source by every student of human biology.

LUTHER BURBANK. *"Our Beloved Infidel." His Religion of Humanity.*
By Frederick W. Clampett.
The Macmillan Co.
$1.50 5 x $7\frac{1}{2}$; 144 *New York*

This is a religious tract, by an Episcopal clergyman, introduced by David Starr Jordan. A perusal of the book leads to the conclusion that Mr. Burbank was an estimable citizen but not a great philosopher.

ZOOLOGY

THE WILD ANIMALS OF AUSTRALASIA. *Embracing the Mammals of New Guinea and the Nearer Pacific Islands.*
By A. S. Le Souef and Harry Burrell, with a Chapter on The Bats of Australia and New Guinea by Ellis Le G. Troughton.
George G. Harrap and Co., Ltd.
25 shillings $5\frac{3}{4}$ x 9; 388 *London*

The authors of this book have done well a useful thing, in providing in one volume a sound working manual of the mammalian fauna of Australia. About 400 species are included. Brief descriptions are given, with a bibliographical reference to at least one source on the form, necessary keys, and 105 photographic illustrations, besides eight text cuts. In addition there are interesting accounts of the habits and habitats of all the more important forms. The Australasian mammalian fauna is, of course, of extraordinary interest to the student of evolution. In the marsupials nearly every adaptation that is found in any other order of mammals has been independently produced. This book furnishes just what the student of evolution needs—a bird's-eye view of the whole order, which he could get only with great difficulty from the scattered sources in which the different forms have been originally described. The resulting picture is bound to make a profound impression on any thoughtful person, because it presents a gigantic and wholly unsolved problem. This book ought to be in every biological library. The authors are to be congratulated on a fine piece of work.

THE BEAVER. *Its Work and Its Ways.*
By Edward R. Warren.
The Williams & Wilkins Co.
$3.00 $5\frac{3}{8}$ x 8; xx + 177 *Baltimore*

This second monograph in the series sponsored by the American Society of Mammalogists gives an interesting summary of what is known about the natural history of the beaver, with an abundance of original observations and excellent photographic illustrations. Much current mythology about the super-human intelligence of this remarkable animal is exploded. The residue is, however, sufficiently extraordinary to make one wish that a competent comparative psychologist would devote say ten years time to a real study of the intelligence of the beaver. There is a bibliography and an index.

MONOGRAPH OF THE VOLES AND LEMMINGS (MICROTINÆ) LIVING AND EXTINCT. *Vol. I.*
By Martin A. C. Hinton.
British Museum (Natural History)
30 shillings *London*
$5\frac{1}{4}$ x $8\frac{1}{2}$; xvi + 488 + 15 plates

This is a superb piece of taxonomic work, on an extremely difficult group, upon which the author has been intensively laboring for more than 25 years. A considerable part of the difficulty arises from the fact that in many of the Microtinæ, and especially the genus *Arvicola*, "apparently, that is so far as actual observation goes, voles of this genus are animals that never stop growing and never grow old." Fossil as well as living species are described. The first 136 pages are devoted to a masterly discussion of the structure and evolution of the group. The remainder contains an extremely thorough and critical systematic account of the 31 genera of Microtinæ, of which 14 are here revised. The volume has great interest for the student of evolution as well as for the systematic mammalogist.

MEDICAL REPORT OF THE HAMILTON RICE SEVENTH EXPEDITION TO THE AMAZON, IN CONJUNCTION WITH THE DEPARTMENT OF TROPICAL MEDICINE OF HARVARD UNIVERSITY, 1924–1925. *Contributions from the Harvard Institute for Tropical Biology and Medicine, No. IV.*
By Richard P. Strong, George C. Shattuck, Joseph C. Bequaert, and Ralph E. Wheeler.
Harvard University Press
$4.00 $7\frac{1}{2}$ x $10\frac{1}{2}$; xvi + 313 *Cambridge*

The first part of this extensively and beautifully illustrated report, by R. P. Strong, G. C. Shattuck, and R. E. Wheeler, deals with the results of the investigation of various tropical diseases. The second part, by J. Bequaert, is concerned with medical and economic entomology, while the third part is a miscellany of geographical, medical, and zoological investigations, contributed to by G. C. Shattuck, J. H. Sandground, and J. Bequaert. The whole report makes a valuable contribution to tropical biology and medicine.

BIOLOGIE DER HYMENOPTEREN. *Eine Naturgeschichte der Hautflügler.*
By H. Bischoff. *Julius Springer*
Reichsmark 27 *Berlin*
$6\frac{1}{4}$ x $9\frac{1}{2}$; vii + 598 (paper)

We have already noticed in these pages earlier volumes in the series of *Biologische Studienbücher*, of which the present book is the fifth number. It is a comprehensive review of the biology of hymenopterous insects. The topics treated are: structure; taxonomy; phylogeny; distribution; movement; nutrition; respiration and circulation; nervous system; nests; eggs and egg laying; brood husbandry; parasitism; social life; sex life; development; adaptation; diseases. There is a bibliography

of 12 pages, and detailed indices. Altogether Dr. Bischoff has given us a valuable reference work.

DELINEATIONS OF AMERICAN SCENERY AND CHARACTER.
By John James Audubon.
Simpkin, Marshall, Hamilton, Kent and Co.
$4.50 6 x 9¼; xlix + 349 *London*

In this book are collected for the first time in a single volume, and in modern (and excellent) typographical dress, the essays which Audubon interspersed between the plates, in his *Ornithological Biography*, under the titles of "Episodes" or "Delineations of American Scenery and Character." There is a sympathetic, though critical, estimate of Audubon's life and work by Professor Francis Hobart Herrick as an introduction. The whole is a useful addition to the literature of biological history. Unfortunately there is no index, which greatly impairs the usefulness to the student of a book of this character.

LE COMMUNISME CHEZ LES INSECTES.
By E.-L. Bouvier. *Ernest Flammarion*
13 francs 4⅝ x 7⅜; 291 (paper) *Paris*

A discussion of the biology of social insects, having for its object the discovery of the spirit which animates such societies. The general conclusion reached is that insect societies are, like human societies, the expression of two kinds of psychological forces, the first instinctive, to which each individual responds blindly, the second plastic and more or less intelligent, permitting the individual to have some initiative in adapting his acts to the circumstances.

THE ELEMENTS OF GENERAL ZOOLOGY. *A Guide to the Study of Animal Biology Correlating Function and Structure, with Notes on Practical Exercises.*
By William J. Dakin.
Oxford University Press
$4.00 5½ x 8½; xvi + 496 *New York*

In this elementary textbook emphasis is laid primarily upon function rather than structure. This method of teaching the subject is apparently more novel, at the moment, in England than it is with us. Laboratory directions are incorporated in the text. American teachers can get some helpful suggestions from the book.

ÜBER GRENZEN DES WACHSTUMS.
By Richard Hesse. *Gustav Fischer*
Mk. 2 6⅝ x 9¼; 36 (paper) *Jena*

A detailed presentation of comparative anatomical evidence in support of the argument that the body size of an animal is a function (in the mathematical sense) of the area of the epithelial surface of the intestine. Most of the data relate to invertebrates. The author does not overlook the fact that other factors are concerned in the determination of body size.

FAUNE CAVERNICOLE DE LA FRANCE. *Avec une Étude des Conditions d'Existence dans le Domaine Souterrain.*
By René Jeannel. *Paul Lechevalier*
75 francs 6½ x 10; 334 (paper) *Paris*

This part of *Encyclopédie Entomologique* is a fine piece of ecological work on cave faunas. The first section, dealing with general ecological conditions and faunal relations in caverns, is followed by a detailed taxonomic list of the invertebrate fauna of French caves.

BOTANY

MANUAL OF CULTIVATED TREES AND SHRUBS HARDY IN NORTH AMERICA. *Exclusive of the Subtropical and Warmer Temperate Regions.*
By Alfred Rehder. *The Macmillan Co.*
$10.50 *New York*
$5\frac{1}{2} \times 8\frac{1}{2}$; xxxvii + 930

This book gives detailed taxonomic descriptions of over 2500 species (with their varieties) of cultivated trees and shrubs, in which category are included also woody vines, bamboos, cacti, and suffruticose plants. It is intended to serve the same purpose as Gray's Manual in the field covered. The work is extremely well done, and should long serve as a valuable reference work, not only to professional botanists, but to gardeners, nurserymen, and tree lovers generally.

ÖKOLOGIE DER ASSIMILIERENDEN HÖHLENPFLANZEN.
By Friedrich Morton.
Urban und Schwarzenberg
6 marks *Berlin*
$6\frac{3}{4} \times 9\frac{1}{2}$; 84 + 3 plates (paper)

This is a worthy companion on the botanical side to the French treatise on cave fauna, noticed elsewhere in this issue of THE QUARTERLY REVIEW OF BIOLOGY. The adaptations, both morphological and physiological, of plants to cave life are extraordinarily interesting. There is a selected bibliography covering 7 pages.

BIOLOGIE DE LA CELLULE. ÉVOLUTION DES CHROMATINES. *Leurs rapports entre elles et avec la cinèse. 1. Dans le tige aérienne de l'Equisetum arvense L. 2. Dans le sac embryonnaire du Fritillaria imperialis L. (Divisions I et II).*
By Maurice Lenoir. *Gaston Doin et Cie.*
55 francs $6\frac{1}{2} \times 10$; 207 (paper) *Paris*

The subject matter of this cytological investigation, which constitutes *Fascicule 26* of the *Archives de Morphologie Générale et Expérimentale*, is sufficiently indicated by the title.

ÜBER KÜNSTLICHE BLATT- UND BLÜTENMETAMORPHOSEN BEI DER SCHNEEBEERE (*Symph. rac. Michx.*) (*Nebst Versuch einer charakterologischen Analyse pflanzlicher Lebensfunktionen*).
By Hans André. *Gebrüder Borntraeger*
10.50 marks *Berlin*
$6\frac{1}{2} \times 10$; vii + 125 + 2 plates

An interesting contribution to the physiological morphology of *Symphoricarpus racemosus*.

OBSERVATIONS ON THE GRASSLANDS OF THE CENTRAL UNITED STATES. *Ohio State University Studies. Contributions in Botany No. 178.*
By John H. Schaffner.
Ohio State University Press
$1.25 $6\frac{1}{2} \times 10$; 56 (paper) *Columbus*

An ecological study.

SOIL CONDITIONS AND PLANT GROWTH.
By Edward J. Russell.
Longmans, Green and Co.
$6.50 $5\frac{1}{4} \times 8\frac{1}{2}$; viii + 516 *New York*

The fifth edition of what has now become an agricultural classic. Owing to the rapid advancement of the subject since 1921 it has been necessary to rewrite all except the historical portions of the

book. It is, in its present form, a work of great general biological interest, as well as a standard reference text for the agriculturist.

POSSIBILITIES FOR PARA RUBBER PRODUCTION IN NORTHERN TROPICAL AMERICA. *Department of Commerce, Bureau of Foreign and Domestic Commerce. Trade Promotion Series No. 40.*
By John C. Treadwell, C. Reed Hill, and H. H. Bennett. *Government Printing Office*
65 cents *Washington, D. C.*
$5\frac{3}{4} \times 9\frac{1}{4}$; xii + 375 (paper)

An interesting contribution to applied ecology, which no botanical library should lack, considering its very moderate price.

MORPHOLOGY

CONTRIBUTIONS TO EMBRYOLOGY. *Vol. XVIII, Nos. 90 to 97. (Publication No. 363). No. 90. Cultivation of Embryonic Heart-Muscle, by Warren H. Lewis. No. 91. Correlation of External Genitalia and Sex-Glands in the Human Embryo, by Karl M. Wilson. No. 92. The "Miller" Ovum—the Youngest Normal Human Embryo thus far Known, by George L. Streeter. No. 93. Detailed Form of the Wolffian Body in Human Embryos of the First Eight Weeks, by Jujiro Shikinami. No. 94. Lens Ectoderm and Optic Vesicles in Allantois Grafts, by Vera Danchakoff. No. 95. Menstrual Records and Vaginal Smears in a Selected Group of Normal Women, by Jessie L. King. No. 96. Transformation of Mononuclear Blood-Cells into Macrophages, Epithelioid Cells in Hanging-Drop Blood Cultures from Lower Vertebrates, by Margaret R. Lewis and Warren H. Lewis. No. 97. Origin of Thrombocytes and of the Different Types of Blood-Cells as Seen in the Living Chick Blastoderm, by S. Sugiyama.*
Carnegie Institution of Washington
$5.75 *Washington, D. C.*
$9\frac{1}{4} \times 11\frac{1}{2}$; 148 (paper)

This volume, with its beautiful plates, well maintains the high standard to which we are accustomed in the output of the Department of Embryology of the Carnegie Institution. Papers No. 90, 91, 92, 94, 95, and 96 are of noteworthy *general* biological interest. Perhaps the most important discovery recorded in the volume is that of the Lewis family (Paper No. 96) to the effect:

"(1) That the mononuclears, macrophages, and epithelioid cells are merely different phases of the same cell type.

"(2) That the transformation of the mononuclears into macrophages, epithelioid cells, and transition forms can scarcely be considered as a true differentiation into new and fixed types of cells.

"(3) That these different forms are more in the nature of temporary functional variations of the same cell type."

ANATOMICAL TEXTS OF THE EARLIER MIDDLE AGES. *A Study in the Transmission of Culture. With a Revised Latin Text of Anatomia Cophonis and Translations of Four Texts. Carnegie Institution of Washington Publication No. 364.*
By George W. Corner.
Carnegie Institution of Washington
$1.00 *Washington, D. C.*
$6\frac{3}{4} \times 10$; 112 (paper)

Professor Corner has not hitherto been known as a medical historian, but this volume will firmly establish his reputation in that field. It is a thorough piece of work, intelligently conceived and critically carried out, and is an important contribution to the history of science, quite

beyond its value in the narrower field of medical history. There has long been an argument as to whether the trained scientific worker could write the history of science better than the trained historian who decided to choose the history of science as his particular field of research. Dr. Corner's book furnishes heavy ammunition for those who take the former position.

THE SPINY DOGFISH. *A Laboratory Guide.*
By Alvin R. Cahn. *The Macmillan Co.*
\$1.10 $4\frac{3}{4}$ x $7\frac{1}{2}$; xii + 94 *New York*
THE SKATE, *Raja erinacea Mitchill. A Laboratory Manual.*
By Charles W. Creaser. *The Macmillan Co.*
90 cents $4\frac{3}{4}$ x $7\frac{1}{2}$; x + 57 *New York*
NECTURUS. *A Laboratory Manual.*
By L. A. Adams. *The Macmillan Co.*
\$1.00 $4\frac{3}{4}$ x $7\frac{1}{2}$; vii + 72 *New York*

These three laboratory guides for the dissection of lower vertebrates, widely used in class work in comparative anatomy, follow traditional lines.

VARIATIONS IN THE FORM OF THE JAWS. *With Special Reference to Their Etiology and Their Relation to the Occlusion of the Dental Arches.*
By J. Sim Wallace. *William Wood and Co.*
\$6.00 $6\frac{1}{4}$ x $9\frac{1}{2}$; xii + 265 *New York*

It is wonderful to observe the growth of specialism in science. Probably no branch of the practice of medicine has, on the whole, been more expressive of the spirit of a technical art, and less animated by what we like to think of as the real soul of science, than has dentistry. But times change. Here is a scientific analysis of one of the categories of biological phenomena which make trouble for dentists. The anatomist will find it a stimulating and useful book. It received the Cartwright Prize.

A SYNOPSIS OF THE GENERAL MORPHOLOGY OF ANIMALS.
By Edwin Grant Conklin.
Princeton University Press
\$1.50 *Princeton, N. J.*
$5\frac{3}{4}$ x $8\frac{1}{2}$; ix + 85

A masterly presentation of the broad facts and principles of animal morphology, with extreme conciseness and clarity. We know of no book in the whole literature of zoology which does so well what this one accomplishes in so little space.

PHYSIOLOGY

MÉTABOLISME DE L'EAU. *Œdèmes—Diurèse—Les Thérapeutiques Hydriques.*
By Marcel Labbé and P.-L. Violle.
Masson et Cie.
28 francs 6 x 9; 256 (paper) *Paris*

This is an excellent presentation of the French point of view in regard to the physical and chemical conditions that determine the amount of water held in the tissues at any one time, and as such it will be of value to the many who are now becoming interested in this highly important branch of biochemistry. One only regrets that, like so many of their countrymen, the authors either ignore or belittle the many contributions to the subject made by investigators in Germany, England, and America. One wonders sometimes whether this sort of thing is done mainly because a writer is not willing to take the word of a foreigner or to give him credit, or because he cannot read any language but his own.

TEXTBOOK OF COMPARATIVE PHYSIOLOGY.

By Charles Gardner Rogers.

McGraw-Hill Book Co., Inc.

$5.50 $5\frac{3}{4}$ x 9; xvi + 635 *New York*

A useful textbook of general physiology on a comparative basis. There is a bibliography of 30 pages and a detailed index. The book is well illustrated and constitutes a valuable addition to the text book literature of general biology.

L'EXCITABILITÉ EN FONCTION DU TEMPS. *La Chronaxie, sa signification et sa mesure.*

By Louis Lapicque.

Les Presses Universitaires de France

45 francs 6 x $9\frac{1}{4}$; 371 *Paris*

A critical review, by the professor of general physiology at the Sorbonne, of the present state of knowledge regarding the time relations in the response to stimuli of a nerve-muscle preparation. The treatment is extremely thorough, from the historical, experimental, theoretical, and methodological standpoints. There is a bibliography covering five pages.

GLYCOGÉNE, ADRÉNALINE ET INSULINE.

By M. Jacot. *Masson et Cie.*

35 francs 6 x 9; 210 (paper) *Paris*

This is a readable discussion of some experiments designed to show the physico-chemical relationships between glycogen, adrenalin, and insulin. They started from the observations (1), that adrenalin when added to a sol of glycogen will reduce the size of the particles and will remove the turbidity; (2), that glycogen acts on adrenalins as an oxidizing agent; and (3), that insulin has a tendency to flocculate glycogen.

Unfortunately, like many other men who come forward with interesting observations and theories, Jacot largely ignores what others have done on his problem; he fails to place his contribution in its proper relation to all that has gone before, and he leaves all but his most highly specialized readers wondering whether they have heard something new or something already disproved.

PHYSIK UND CHEMIE DES RADIUM UND MESOTHOR. *Für Ärzte und Studierende.*

By Albert Fernau. *Julius Springer*

Rm. 7.50 *Wien*

6 x 9; v + 101 (paper)

The second edition of a useful elementary text on the biophysics of radioactive substances. The treatment is very concise, but clear, and the information is presented with a minimum of mathematics. There is a short bibliography appended, but no index.

THE SCIENTIFIC FEEDING OF ANIMALS.

By O. Kellner (Authorized translation by William Goodwin).

Gerald Duckworth and Co.

8 s. 6 d. $4\frac{3}{4}$ x $7\frac{1}{4}$; xiii + 328 *London*

A second English edition of a well-known, standard text in the field of animal nutrition. A chapter on vitamins and a fuller discussion of the making of silage are the most important additions.

BEWEGUNGEN UND INNERVATION DES WIEDERKÄUERMAGENS.

By E. Mangold and W. Klein.

Georg Thieme

3.60 marks $6\frac{3}{4}$ x 10; 58 (paper) *Leipzig*

An interesting experimental contribution to the physiology of the vegetative nervous system.

BIOCHEMISTRY

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 218.* FERMENTFORSCHUNG. *Containing following articles: Darstellung polypeptidspaltender Fermentsole aus Hefe und Pankreas, by Andor Fodor and A. Bernfeld; Esterasen, by Peter Rona; Carboxylase, by Carl Neuberg; Sulfatase, by Carl Neuberg and Joachim Wagner; Abfangverfahren, by Carl Neuberg and Maria Kobel; Phosphatasen, by Carl Neuberg and Ernst Simon; Carboligase, by Carl Neuberg and Maria Kobel; Phytochemische Reduktionen, by Carl Neuberg and Günther Gorr; Die Methylenblaumethode zum Studium der biologischen Oxydationen, by Gunnar Ahlgren.*

Urban und Schwarzenberg
Mk. 9 7 x 10; 187 (paper) *Berlin*

HANDBUCH DER BIOLOGISCHEN ARBEITSMETHODEN. *Lieferung 220. Methoden der mikrobiologischen Bodenforschung.*
By Selman A. Waksman.

Urban und Schwarzenberg
Mk. 7.20 7 x 10; 150 (paper) *Berlin*

The first of these two numbers of the Abderhalden handbook appeals only to workers in rather restricted special fields of biology, but Dr. Waksman's contribution, which is a very thorough exposition of the technique of soil microbiology, has possibilities of interest to the general biologist, who has, generally speaking, rather neglected the possibilities of the soil to furnish useful material for laboratory investigations.

SULFUR METABOLISM. *A Review of the Literature.*
By Max Kahn and Frederic G. Goodridge.

Lea and Febiger
\$9.00 *Philadelphia*
$5\frac{3}{4}$ x $9\frac{1}{4}$; xiv + 831

This solid, substantial reference work fittingly serves, as the authors suggest in the preface, to complete the trilogy of review treatises on metabolism, which began with Atwater and Langworthy's *Digest of Metabolism Experiments*, followed many years later by Forbes and Keith's *Phosphorus Compounds in Animal Metabolism*. The compilation of this volume on sulphur was obviously a colossal task. But the authors will have the blessing of students for a long time to come. The thoroughness of the treatment is evident in the first chapter. It includes 135 pages and is devoted to the literature on the sulphur content of the various organs, tissues, and fluids of the body, exclusive of the urine.

LEHRBUCH DER PHYSIOLOGISCHEN UND PATHOLOGISCHEN CHEMIE. *In 75 Vorlesungen, für Studierende, Ärzte, Biologen und Chemiker. I. Band: Organchemie. III. Lieferung: Organe mit Innerer Sekretion, Geschwülste. Vorlesung: XXX bis XL.*
By Otto Fürth. *F. C. W. Vogel*
Marks 15 *Leipzig*
7 x 10; v + 166 (paper)

This part of the Fürth textbook, earlier portions of which have been previously noticed in THE QUARTERLY REVIEW OF BIOLOGY, is of particular interest to the general biologist, because it includes a discussion of the biochemistry of the sex organs and of embryonic development, along with the treatment of other organs of internal secretion.

THE DETERMINATION OF HYDROGEN IONS. *An Elementary Treatise on the Hydrogen Electrode, Indicator and Supplementary Methods with an Index Bibliography on Applications.*
By W. Mansfield Clark.
The Williams & Wilkins Co.
$5.00 6 x 9; 480 *Baltimore*

This second edition of the standard American text on hydrogen ion technique has been considerably rewritten and brought up to date. Nine hundred new titles have been added to the bibliography, bringing the total up to over 2000.

LEITFADEN FÜR BIOCHEMISCHE MIKROMETHODEN. *Als Laboratoriumsbuch zusammengestellt für das Biochemische Laboratorium der Vereinigten Fabriken für Laboratoriumsbedarf von deren wissenschaftlichem Beirat.*
By Paul Ruszczynski.
Vereinigten Fabriken für Laboratoriumsbedarf Ges. m. b. H.
Reichsmark 3 7 x 10; 163 *Berlin*

An apparatus catalogue, annotated to show how the apparatus is to be used. This is a good idea, which might profitably be extended to other fields than biochemical micro-technique.

SEX

SEX FREEDOM AND SOCIAL CONTROL.
By Charles W. Margold.
The University of Chicago Press
$2.00 $5\frac{1}{4} \times 7\frac{5}{8}$; xi + 143 *Chicago*

This book attacks one of the main roots of birth-control philosophy. Its principal thesis is that the "distinction between sexual relations that result in offspring—and therefore held as social—and sexual relations that do not result in procreation—and therefore urged as individual—is not sound."

It is concluded, after a very heavily documented sociological and anthropological discussion (the bibliography runs to 486 titles) that "due to the special importance of sex matters in man's life, individuals and groups can, as a matter of conscious planning, relinquish the intentional or higher-control phases in sex, only at their peril. They neglect the purposive safekeeping, from generation to generation, of the social heritage in regard to sex conduct, only at their own undoing. It seems probable, therefore, as to the future, that social control will continue, even on its more organized levels, purposively to institute group modes of sex conduct, and to insist upon them when necessary, together with other means, also through legislative enactment and state enforcement."

We greatly fear that the whole tenor of this treatise is counter to the philosophy of the "youth" movement which seems the most striking social phenomenon of the present time all over the world. And it must be confessed that the last clause of the last sentence quoted has an ominous sound. Reginald, our office boy, offered to bet the janitor 6 to 5 that Professor Margold is an active, due-paying member of the Anti-Saloon League, but fortunately this shocking proposal was overheard and both malefactors were disciplined.

CONTRE FREUD. *Critique de Toute Psychologie de l'Inconscient.*
By Jean Bodin. *Masson et Cie.*
14 francs *Paris*
$6\frac{1}{2} \times 9\frac{3}{4}$; iv + 99 (paper)

A treatise preliminary to a larger work

on personality. In preparing this the author found it desirable to clear the ground of prior, and in his opinion, unsound theories. Hence this volume, which is a detailed critique of Freud, in some points penetrating and sound.

DIE WIRKUNGSWEISE ABGESTUFTER KEIMDRÜSENSCHÄDIGUNG. *Eine experimentelle Studie zur Frage der endokrinen Sexualfunktion.*
By Heinrich Viktor Klein.
Urban und Schwarzenberg
Marks 12 *Berlin*
7 x 10; vi + 144 (paper)

After a review of the literature covering 80 pages the author gives an excellent account of his own experiments on guinea pigs and rabbits, involving castration, autoplastic transplantation of gonads, ligature of the vas deferens, X-ray radiation of the gonads, and partial removal of radiated gonads. The conclusions from what seems to have been a careful and critical piece of work are extremely interesting, but too voluminous to present here. One point only may be noted: neither ligation of the vas nor X-ray radiation of the gonads produced any constant, marked, or permanent increase in interstitial cells.

BIOMETRY

DAS EXPONENTIALGESETZ ALS GRUNDLAGE EINER VERGLEICHENDEN BIOLOGIE.
By Ernst Janisch. *Julius Springer*
Reichsmark 28.20 *Berlin*
$6\frac{1}{4}$ x $9\frac{1}{2}$; iv + 383 (paper)

An enormously painstaking review of the great range of biological phenomena which, in whole or in part, and in greater or smaller degree, follow the law of compound interest in their quantitative relations, in one or another of its forms. There is a bibliography covering some 10 pages. The book will be a useful reference source in any biological research laboratory.

PSYCHOLOGY AND BEHAVIOR

THE MEASUREMENT OF INTELLIGENCE.
By Edward L. Thorndike, E. O. Bregman, M. V. Cobb, Ella Woodyard, and the Staff of the Division of Psychology of the Institute of Educational Research of Teachers College, Columbia University.
Teachers College, Columbia Univ.
$4.00 6 x 9; xxvi + 616 *New York*

The position of the authors is that: "An intellectual task is one, success in which depends upon all of intellect and nothing but intellect. Intellect is definable by a series of tasks, and we have so defined one variety of it, Intellect CAVD, and could so define any other variety of it. A CAVD intellectual task is, then, one success at which depends upon all of Intellect CAVD and nothing but Intellect CAVD. Tasks can be devised which do substantially meet this requirement, success at one of them correlating perfectly (or as closely as its own self-correlation permits) with success in the entire series."

The tasks upon which intellect CAVD is defined are:

"C. To supply words so as to make a sentence true and sensible.

"A. To solve arithmetical problems.

"V. To understand single words.

"D. To understand connected discourse as in oral directions or paragraph reading."

The book is a detailed technical account of an extensive investigation of intellect CAVD. Its significance at this stage of the development of the subject seems to be chiefly methodological.

THE FATHER IN PRIMITIVE PSYCHOLOGY.

By Bronislaw Malinowski.

W. W. Norton and Co., Inc.

\$1.00 $4\frac{1}{4} \times 6\frac{1}{2}$; 95 *New York*

This little book is a joy. Written with consummate skill and deep knowledge, it describes the psychology of the natives of the Trobriand Islands regarding the physiology of human and animal reproduction, and the social consequences which flow from their incomplete knowledge of this subject. They believe that the male has no significant physiological part in reproduction, and the cogency of the arguments with which they support this view is a delight. This doctrine is basically embodied in their whole social organization. Perhaps the most entertaining thing about it all is that by every pragmatic test the whole system works just as well, though founded on this plain biological error, as do systems founded on its truthful antithesis. One is tempted to enquire about the price of pragmatism, considered as a test of "truth."

THE NATURAL HISTORY OF OUR CONDUCT.

By William E. Ritter, with the collaboration of Edna Watson Bailey.

Harcourt, Brace and Co.

\$3.50 $5\frac{3}{4} \times 8\frac{1}{2}$; ix + 339 *New York*

Anything that Professor Ritter writes is sure to be interesting and provocative of thought. The latest volume is no exception. It is an extraordinarily entertaining attempt at a consistent exposition of what might perhaps be called phylogenetic behaviorism. Applying essentially that type of reasoning which was characteristic of the good old science of comparative morphology, with of course intelligent modifications suitable to the nature of the subject, the author brings together a mass of evidence showing how the activities of lower animals form a graded series which can be interpreted as steps in an evolutionary process which culminates in human behavior. However much one may disagree with details of its conclusions or its philosophy, this is a stimulating book, well worth the attention of every biologist. It includes a bibliography of four pages, and a detailed index.

THE MIND AND ITS MECHANISM. *With Special Reference to Ideo-Motor Action, Hypnosis, Habit and Instinct, and the Lamarckian Theory of Evolution.*

By Paul Bousfield and W. R. Bousfield.

E. P. Dutton and Co.

\$4.00 $5\frac{1}{2} \times 8\frac{1}{2}$; vii + 224 *New York*

This book sets forth a novel scheme for bridging the psychophysical gap. The authors postulate a new kind of matter, which somewhat paradoxically is stated to be "immaterial." It is composed of "psychons" which are like electrons except that they are different. The psychons make up a "psychic brain" which implements the *liaison* between consciousness and the nervous system. Space lacks for a complete exposition of the theory here. It is undeniably ingenious, but beyond this there seems little to recommend it.

A SHORT OUTLINE OF COMPARATIVE PSYCHOLOGY.
By C. J. Warden.
W. W. Norton and Co., Inc.
\$1.00 $4\frac{1}{4} \times 6\frac{1}{2}$; 96 *New York*

This is a brief history of thought and work on animal behavior, well written, and with penetrating insight. While issued in a popular series, this volume is well worth the attention of serious students.

AN INTRODUCTION TO THE THEORY OF PERCEPTION.
By Sir John Herbert Parsons.
The Macmillan Co.
\$5.25 $6 \times 9\frac{1}{2}$; 254 *New York*

A thorough, critical review, with extensive documentation, of the present state of knowledge of the physiological psychology of man's sense organs. It tells what is known of the biological mechanisms by which man becomes aware of his environment.

DE OMNIBUS REBUS ET QUIBUSDEM ALIIS

THE LOGIC OF MODERN PHYSICS.
By P. W. Bridgman.
The Macmillan Co.
\$2.50 $6 \times 8\frac{3}{4}$; xiv + 228 *New York*

This seems to us to be a great book. Physics is just now in the midst of a period of uninhibited theorizing which has many of the objective attributes of a drunken party. The joys of inebriety are notorious, but unfortunately experience teaches that there is always a "morning after." To remind his colleagues in the domain of physics of this hard and disagreeable fact was, we take it, Professor Bridgman's main object in writing this book. Its philosophical significance, however, is much broader than the science of physics. The biologist, and especially the geneticist, will do well to read and ponder over it.

Dr. Bridgman is an experimentalist of the very first rank. There are very few physicists living who can equal or surpass his record as an experimentalist. The importance of this book lies in the fact that such a man turns a cold, shrewd, and perhaps even slightly bilious eye upon the fundamental concepts of his science, at a time when they are being subjected to a considerable revision every other Tuesday.

It is impossible to do justice to the book in the space that can be devoted to it. Really all we can do is to recommend biologists *to read it*. And that we do most earnestly. It is not precisely easy reading, but this is only because the argumentation is everywhere closely knit, not because of heavy mathematics or other technicalities. The key note of the philosophy of the book is that knowing is doing *et praeterea nihil.*

> What do we mean by the length of an object? We evidently know what we mean by length if we can tell what the length of any and every object is, and for the physicist nothing more is required. To find the length of an object, we have to perform certain physical operations. The concept of length is therefore fixed when the operations by which length is measured are fixed: that is, the concept of length involves as much as and nothing more than the set of operations by which length is determined. In general, we mean by any concept nothing more than a set of operations; *the concept is synonymous with the corresponding set of operations.* If the concept is physical, as of length, the operations are actual physical operations, namely, those by which length is measured; or if the concept is mental, as of mathematical continuity, the operations are mental operations, namely those by which we determine whether a given aggregate of magnitudes is continuous.

This has a refreshing sound, and there is a great deal more of the same invigorating medicine in the book. Read it!

LES CANCERS DU SEIN.
By Pierre Delbet and Mendaro.
Masson et Cie.
50 francs $6\frac{1}{2}$ x 10; 343 (paper) *Paris*

LES CANCERS ET LEURS COMPLICATIONS. *Étude Clinique de Leur Évolution.*
By Maurice Renaud. *Masson et Cie.*
30 francs 6 x $9\frac{1}{4}$; 322 (paper) *Paris*

DIAGNOSTIC DES PRINCIPAUX CANCERS.
By Henri Hartmann (with the collaboration of Mm. Bensaude, Bérard, Chevassu, Darier, Forgie, Legueu, Lemaitre, Michon, Morax, Nové-Josserand, Okinczyc, Rist, Roussy, Sébileau). *Masson et Cie.*
10 francs 6 x $8\frac{3}{4}$; 64 (paper) *Paris*

These volumes concern the medical man rather than the general biologist. All three are eminently practical treatises written with the precision of style for which good French writing is so justly famed. The first two are extensively and well illustrated.

A PSYCHOLOGICAL STUDY OF CANCER.
By Elida Evans. *Dodd, Mead and Co.*
\$2.50 $5\frac{1}{2}$ x 8; viii + 226 *New York*

Psychoanalysts are going to have a lot of answering to do when they are lined up before the Judgment Seat. The author of this treatise is a pupil and follower of Jung. She has psychoanalyzed a number of cancerous persons. From this experience she has generalized, with the results exhibited in this book. It seems that cancer patients are "feeling extraverts, full of life and activity." "That part of the body attacked [by cancer] we have found to have been the seat of the detached libido. In women it is most frequently the maternal organs, as though there had been in the patient an unsatisfied maternity. I am told by the highest authorities that in a certain Asiatic nation cancer of the breast is exceedingly rare. As there is a very rapid increase in the population, and a man is not confined to his wife if he can afford a concubine, there is probably no lack of the nursing satisfaction. . . . .

"Without exception, I have found the life of all cancer patients needed broadening, as plainly seen from the blow to their emotions when detached from their objective attachment."

Somehow we feel that if it were likely that this book would be taken seriously it might do a great deal of harm.

ANTIGÉNOTHÉRAPIE DE LA TUBERCULOSE. *Par les Extraits Méthyliques de Bacilles de Koch.*
By L. Nègre and A. Boquet. Preface by A. Calmette. *Masson et Cie.*
16 francs $5\frac{1}{4}$ x $7\frac{3}{4}$; 158 (paper) *Paris*

An experimental and clinical study of methyl alcohol extracts of tubercle bacilli, preliminarily treated with acetone. Such an extract, freed of its alcohol, and suspended in physiological salt solution, is found to be a potent antigen for the production of tubercular antibodies. Striking results are reported from its use in treating experimental tuberculosis in animals, and also certain forms of human tuberculosis.

ORGANISED PUBLICATION. *A Connected Series of Proposals Relating to the Publication and Record of Scientific and Technical Information.*
B. J. F. Pownall. *Elliot Stock*
5 shillings 6 x $9\frac{3}{4}$; 91 *London*

This book sets forth a carefully thought out scheme for standardization in the publication of scientific literature. Its

most important features are standardization of page size; printing journals so that they may be broken up into the equivalent of reprints; and finally a plan for standardized indexing. While there is nothing particularly novel in the separate suggestions the plan as a whole is worth the careful consideration of scientific men, in trying to solve a problem of ever-increasing difficulty.

LES CONCEPTS SCIENTIFIQUES.

By Hélène Metzger. *Félix Alcan*
12 francs *Paris*
$4\frac{5}{8} \times 7\frac{1}{4}$; xi + 195 (paper)

This is a metaphysical discussion of the problem of classification in general. It received in 1925 the Bordin prize of the *Académie des Sciences morales et politiques*.

HISTORY OF THE SCIENCES IN GRECO-ROMAN ANTIQUITY.

By Arnold Reymond (Translated by Ruth Gheury De Bray). *E. P. Dutton and Co.*
\$2.50 $4\frac{7}{8} \times 7\frac{1}{4}$; x + 245 *New York*

An interesting, but not very important book. The best section is that on the mathematical sciences.

THE COST OF BIOLOGICAL BOOKS IN 1927

By RAYMOND PEARL

Institute for Biological Research, Johns Hopkins University

AT THE end of the first volume of the QUARTERLY REVIEW OF BIOLOGY (Vol. I, pp. 605–608, 1926) was inaugurated the plan of reporting annually on the cost of the books which had been received during the year. The present paper continues this plan with the report of book costs for the year 1927.

For the purpose of price comparison the books are classified by origin as follows:

I. *The United States.* Here are put all books published by strictly, or primarily, American publishers. Naturally the majority of books reviewed during the year have had this origin just as in 1926.

II. *Germany.* In the number of books sent in by publishers for review Germany stands next to this country.

III. *English-American.* In this group are placed the books which are manufactured and published in the first instance in England by publishing houses which have *branches* under their own name (not merely agents) in this country. The American branch imports the books into this country and distributes them here, priced in dollars rather than shillings.

IV. *England.* In this class are placed books published in England, priced in shillings, and available in this country only by direct importation, by the individual or through an agent.

V. *France.* This group includes all books published in France and her colonies.

VI. *Other countries.* Here are placed all books published in any other country than those specified above.

VII. *United States Government.*

VIII. *British Government.* This is a new rubric not separately listed in the 1926 discussion. It has seemed desirable this year to make a separate item for British government publications, on the same ground that United States government publications are treated by themselves. It is unfair to include such publications with books commercially produced.

Table 1 gives, for each of these eight rubrics, (*a*) the total number of pages in the books received for review; (*b*) the total cost of these books in dollars, foreign prices being converted to dollars on the basis of the exchange prevailing when the books were received; (*c*) the average price per page *in cents*.

In order to facilitate comparison between 1926 and 1927 in respect of book prices, table 2 has been prepared. In this table the following items are included: (*a*) the average price per page, in cents, for the year 1926; (*b*) the average price per page, in cents, for the year 1927; (*c*) the absolute change in average price per page, in cents, between 1926 and 1927, a + sign denoting an *increase* in 1927 as compared with 1926, and a − sign denoting a *decrease;* (*d*) the percentage difference of the 1927 average price per page from that of 1926 taken as a base, the + sign again indicating that the

books were on the average higher in price in 1927 than they were in 1926, and the − sign that they were lower.

The data presented in tables 1 and 2 permit some interesting deductions. In the first place it is evident that a larger number of books were noticed in the QUARTERLY REVIEW OF BIOLOGY in 1927 than in 1926. The total number of pages in the books reviewed in 1926 was 82,575, while in 1927 it was 102,109, an increase of 23.7 per cent.

TABLE 1

Prices of biological books, 1927

ORIGIN	TOTAL PAGES	TOTAL COST	PRICE PER PAGE
			cents
English-American	9,013	$125.05	1.39
Germany	18,528	221.70	1.20
England	7,639	87.10	1.14
United States	47,779	522.40	1.09
British Government	2,520	24.18	0.96
Other countries	3,429	26.71	0.78
France	10,805	38.59	0.36
U. S. Government	2,396	5.65	0.24

TABLE 2

Comparison of the prices of biological books in 1926 and 1927

ORIGIN	AVERAGE PRICE PER PAGE 1926	AVERAGE PRICE PER PAGE 1927	ABSOLUTE CHANGE + OR −	RELATIVE CHANGE + or −
	cents	*cents*	*cents*	*per cent*
English-American	1.55	1.39	−0.16	−10.3
Other countries	1.51	0.78	−0.73	−48 3
England	1.28	1.14	−0.14	−10.9
United States	1.12	1.09	−0 03	−2.7
Germany	1.09	1.20	+0.11	+10.0
France	0.35	0.36	+0.01	+2.9
U. S. Government	0.31	0.24	−0.07	−22.6

In 1927 as in 1926 the most expensive books were the English-American on the basis of the average price per page. But, as was pointed out last year, it must be remembered that these books had paid duty. France, this year as last, occupies the lowest position in the list for commercially published books. Its average price per page is lower than that for any other group except the United States government publications.

The most striking change in the 1927 table as compared with that for 1926 is the altered position of Germany. In last year's article the following comment was made:

"There is a widely prevailing impression that the German publishers are greatly over-pricing their products at the present time. This does not seem to be the case, so far as the present sample of new biological books is concerned. Making due allowance for the fact that the majority of the German prices included in the table are for books in paper covers, it turns out that the biological books received from Germany during 1926 cost almost exactly the same per page as those turned out by American publishers."

Table 1 of the present paper indicates that the situation has altered, so far as may be judged from the samples of German books received in 1926 and 1927. This year the German books received, which do not pay duty, had an average price per page second in the list; higher than the price of English books in England, and notably higher than American books published and sold in this country. It would be easy to suggest that the difference between the 1926 and the 1927 average is due to the QUARTERLY REVIEW OF BIOLOGY having received in 1927 an intrinsically different and more expensive class of German books in 1927 than in 1926. But a detailed examination of the books themselves does not support such an explanation. On the whole the books of the two years seem to be equivalent random samples of German scientific books

generally. We shall await with great interest the comparative showing of German biological book prices in 1928.

Table 2 exhibits the gratifying result that, with the exception of those produced in Germany, the biological books comprised in these two samples either remained at the same level of average price per page in 1927 that they held in 1926, or else declined in average price. English and English-American biological books *fell off* in price, so far as may be judged from these samples, by approximately 10 per cent. American and French average prices maintained in 1927 their 1926 level, the changes, down and up respectively, being obviously insignificant, considering the chance errors involved in the sampling. The average price per page of the German biological books here under discussion *increased* 10 per cent in 1927 over 1926. The large percentage decrease in average price of the "other countries" books shown in table 2 probably does not mean much. The samples were small in both years, and the books showed great variation in character and price. It is interesting and pleasing to note that the United States government publications showed a decrease of 22 per cent in average price per page in 1927 as compared with 1926. Is this to be regarded as one result of the "economy program" of the present administration?

If all the books noticed in the Quarterly Review of Biology in 1926, regardless of origin, are lumped together and compared with all the books noticed in 1927 it works out that the average price per page in 1926 was 1.097 cents, and 1.030 cents in 1927. This indicates a *decrease* in average price per page of just over 6 per cent.

In concluding these notes for the present year I should like to emphasize that the statistical nature of the basic data is such as not to permit wide generalization. We are dealing here only with very small samples of books in general, and with by no means all of the strictly biological books. Indeed for some of the countries our samples are only small fractions of the biological works there published. So the reader must be cautious in the kind of conclusions he draws from these annual reviews of the experience of the Quarterly Review of Biology regarding book prices.

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